AN ANALYSIS OF THE *CORDYLUS POLYZONUS* COMPLEX (REPTILIA: CORDYLIDAE) IN THE SOUTH-WESTERN CAPE

by

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(with 21 text figures and 3 tables)

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DECLARATION

I the undersigned hereby declare that the work contained in this thesis is my own original work and has not previously in its entirety or in part been submitted at any university for a degree.

NCBadenhorst .... 25-01-1990 ....

Signature   Date

This thesis is presented in the form of three separate sections each prepared as a complete article ready for publication. Inevitably there is some degree of overlap between the sections, but it must be remembered that each section is to be published in isolation. For the benefit of the reader a short summary is given which highlights the major aims and findings of my research. Alternatively, for a quick overview, the reader can consult the short abstract at the beginning of each section. My study-leaders are listed as co-authors for all three articles.

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SUMMARY

Mouton and Oelofsen (1988) suggested that melanistic cordylid populations in the south-western Cape represent relict, cold-adapted populations which evolved under adverse climatic conditions during the Last Glacial Period, 18 000-16 000 BP. The first section of this study was undertaken to test their model for the evolution of melanism in the cordylid species, Cordylus polyzonus. For this purpose, geographic character variation among populations of Cordylus polyzonus in the region south of 32°15' latitude and west of 19°15' longitude was investigated. Variation in 122 external morphological characters was analysed in 306 specimens from 93 localities. Although no inter-locality variation was observed in most of the characters, a high degree of concordancy was observed in the geographical variation of three headshield characters. These three headshield characters are considered non-adaptive and can accordingly be regarded as good indicators of genealogical relationship. Since they varied together with other adaptive characters such as melanism and body size, it can be concluded that geographically isolated melanistic populations of Cordylus polyzonus represent relicts of a once larger melanistic population. The data underscore the Mouton-Oelofsen hypothesis for the evolution of melanistic cordylid taxa in the south-western Cape.

A further corrolary of the Mouton-Oelofsen hypothesis, is that melanistic cordylids are presently restricted to cool enclaves. This assumption was evaluated in the second section of this study by analysing prevailing climatic conditions associated with the occurrence of extant melanistic populations of the genera Cordylus and Pseudocordylus in the south-western Cape. Climatic data were obtained from 123 weather stations in the study-area. A close correspondence was found between the distribution of melanistic populations along the westcoast and the primary upwelling zones of the southern Benguela Current. Lower mean daily temperatures and a high incidence of advective sea fog on the adjacent coastal regions are direct effects of these cold upwelled waters. Likewise, montane melanistic populations, occurring at relatively high altitudes along the extreme western borders of the Cape Fold Mountains, also experience lower mean daily temperatures and a high incidence of orographic fog and cloud cover. Melanistic cordylid populations therefore generally have to

contend with relatively exposed environmental conditions of low temperature and limited solar radiation due to the filtering effect of fog and cloud cover. The fact that all the melanistic taxa in this region occur as small isolated populations limited to cool enclaves, suggests that they are presently in a contracted state under strong environmental pressure. It is postulated that palaeoclimatic conditions very similar to climatic conditions presently prevailing in these enclaves were experienced over the entire western coastal region, at least as far as the Orange River, during the Last Glacial Maximum when melanism probably evolved. Our results therefore corroborate the Mouton-Oelofsen hypothesis that isolated melanistic cordylid populations represent cold-adapted relicts.

One would accordingly expect melanistic populations to posses some enhanced ability to absorb infrared radiant heat to cope with these conditions of limited sunshine and lower temperatures. In section three of this study, differences in dorsal skin reflectivity between melanistic and turquoise C. polyzonus populations were quantified. Furthermore, the physiological ability of this species to change body colour was investigated, as well as ontogenetic colour change. Significant differences in dorsal skin reflectivity existed between melanistic and turquoise specimens in the 500-1300 mμ spectral range, demonstrating the greater heat-absorbing capacity of melanistic populations. The data underscore the Mouton-Oelofsen model that melanistic populations are "cold-adapted" relicts. Furthermore, ontogenetic colour change is a real phenomenon in the melanistic variation of C. polyzonus. In this respect it is unique among the melanistic cordylid taxa in that ontogenetic colour change seemingly does not occur in the other forms. Experiments to investigate short term colour change in response to different temperatures regimes, produced no conclusive results. On the other hand, seasonal colour changes could be demonstrated for both melanistic and turquoise specimens, indicating that this species has the physiological capacity to change colour. It is, however, believed that geographic colour variation in C. polyzonus cannot be attributed to this capacity, but is rather the result of selection over time. This view is underscored by the results of section one demonstrating that, apart from colour and body size, melanistic and turquoise forms also differ in certain non-adaptive traits, suggesting that they do not belong to the same primary gene pool.

AN ANALYSIS OF GEOGRAPHIC CHARACTER VARIATION IN THE KAROO GIRDLED LIZARD, *CORDYLUS POLYZONUS*, IN THE SOUTH-WESTERN CAPE, SOUTH AFRICA

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In order to test the hypothesis that melanistic cordylid populations in the south-western Cape are relict populations, character variation among populations of the Cordylus polyzonus complex in the section of the Cape Province south of $32^{0}15'$ latitude and west of $19^{0}15'$ longitude was analysed. Variation in 122 external morphological characters among 93 localities was determined. Concordant patterns in the distribution of adaptive as well as non-adaptive characters were observed. The data were interpreted as indicating that melanistic C. polyzonus populations in the area belong to the same primary gene pool suggesting that they are remnants of a once larger melanistic population.

Ten einde die hipotese dat melanistiese gordelakkedis populasies in die suidwes-Kaap reliekpopulasies is, te toets, is eienskapvariasie tussen populasies van die Cordylus polyzonus kompleks in die deel van die Kaapprovinsie suid van $32^{0}15'$ breedtegraad en wes van $19^{0}15'$ lengtegraad ondersoek. Variasie in 122 uitwendige morfologiese kenmerke tussen 93 lokaliteite is bepaal. Ooreenstemmende patrone in die verspreiding van adaptiewe sowel as nie-adaptiewe kenmerke is waargeneem wat vertolk word as aanwysend dat melanistiese C. polyzonus populasies in die gebied tot dieselfde primêre genepoel behoort. Dit suggereer dat die melanistiese populasies oorblyfsels is van 'n eens groter melanistiese populasie.

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INTRODUCTION

Mouton (1986) and Mouton and Oelofsen (1988) suggested that melanism in cordylid species in the south-western Cape evolved as an adaptation to adverse climatic conditions during the Last Glacial Period, 18 000-16 000 BP. Based on an analysis of geographical character variation in the common Cape girdled lizard, Cordylus cordylus (Mouton 1987), Mouton and Oelofsen (1988) came to the conclusion that melanistic populations of the Cordylus cordylus complex in the south-western Cape represent relict, cold-adapted forms. According to their model, vicariance of an ancestral warm-adapted population occurred with the onset of cooler climatic conditions during the Last Glacial Maximum, the Cape Fold Mountains acting as the cutt-off zone. With the lowering of the sea-level (Tankard 1976) and resultant increased influence of the Cold Benguela Current on the climates of the south-western coastal lowlands, the daughter population to the west of the Cape Fold Mountains became subjected to more adverse climatic conditions than the inland daughter population east and south-east of the Cape Fold Mountains. Melanism evolved in the western population in response to the harsh conditions, while the eastern inland population remained warm-adapted. This event probably allowed the melanistic population to rapidly expand its range during the cooler conditions which prevailed along the western coastal lowlands.

With the amelioration of the climates after 16 000 BP, the now cold-adapted melanistic population west of the Cape Fold Mountains fragmented, finally remaining only in suitable cool enclaves, either along the westcoast or along the western flank of the Cape Fold Mountains. The warm-adapted inland population, on the other hand, underwent a rapid range expansion, eventually penetrating into the western coastal lowlands, an area formerly occupied by the cold-adapted populations. Subsequently zones of secondary contact between the remaining cold-adapted melanistic populations and the warm-adapted form were established.

Mouton and Van Wyk (1990) described the melanistic montane form as a new species, Cordylus oelofseni, and elevated the coastal melanistic form, previously described as a subspecies of C. cordylus, to a full species, C. niger. Because C. niger and C. oelofseni share several character states they maintain that these two species are sister taxa.

Before attempting the reconstruction of the biogeographical history of a species, it is, however, essential to identify all the monophyletic groups showing congruent distribution patterns in the study-area (Wiley 1981). According to adherents of vicariance biogeography (Rosen 1978; Nelson and Platnick 1980; Brown 1982; Cracraft 1982; Endler 1982; Vrba 1985) such congruency probably indicates the same biogeographical history for all the concerned groups. Mouton amd Oelofsen (1988) maintain that one way of testing their proposed model for evolution in the C. cordylus complex, is to look for concordant patterns in other closely related species. Mouton (1986) has already established that there is a high incidence of melanistic cordylid populations along the south-western coastal regions and pointed out the high degree of concordancy in the geographical occurrence of melanistic populations of different species. The Mouton-Oelofsen hypothesis that the melanistic cordylid populations are relicts of larger melanistic populations which prevailed during the Last Glacial Period can be falsified by showing that melanistic and non-melanistic populations of cordylid species in the area belong to the same primary gene pool, in other words that melanistic populations represent ecotypes. The Karoo girdled lizard, Cordylus polyzonus, is one of those cordylid species in the south-western Cape which forms a complex comprising both melanistic and non-melanistic representatives. In fact, four colour variations of the nominate species occur in this region (Figure 1), some of which also extend into areas outside the western Cape.

In the area between St. Helena Bay and Saldanha Bay, a melanistic population occurs where individuals mainly inhabit coastal rock, although they are found a few kilometers inland as well. Small melanistic populations of this species also occur higher up the south-western coast at Verlorenvlei near Elands Bay, along river banks near Lamberts Bay, and at the Buchu Twins near Alexander Bay (Mouton 1986). Outside the study-area, melanistic populations has been recorded from regions in the south-eastern Orange Free State and the north-eastern Cape (FitzSimons 1943; De Waal 1978).

The south-western coastal lowlands are mainly inhabited by a much larger turquoise form. Mouton (1986) reported that this form was never found within a few kilometers from the coast and nowhere at high altitudes. Furthermore, he noted the borders between adjacent melanistic and turquoise populations in the vicinity of Saldanha Bay to be sharp with no apparent transition between the two colour variants. From Piketberg northwards to Little Namaqualand, the body colour of the lizards becomes darker to different shades of brown. In the Worcester-Villiersdorp area, individuals are reddish in colour.

It would be appropriate at this stage to highlight similarities between the Cordylus cordylus and Cordylus polyzonus-complexes. In Figures 1 & 2., the distribution patterns of the different morphotypes of the Cordylus polyzonus an Cordylus cordylus-complexes are depicted, respectively. Striking resemblances can be seen in the distribution patterns of the different taxa of the two complexes. In both cases, melanistic populations are confined either to sea-facing situations along the south-western coast or to localities of relatively high altitude along the Cape Fold Mountains. Without exception the distribution patterns of melanistic populations are disjunct and geographically isolated. Furthermore, the areal extent of melanistic Cordylus polyzonus and Cordylus niger populations coincides almost exactly in the Saldanha Bay area. Non-melanistic populations of both complexes, on the other hand, are generally widespread, especially along the coastal lowlands. These similarities led Mouton and Oelofsen (1988) to the conclusion that non-melanistic cordylid populations in the south-western Cape represent expanding warm-adapted forms, whilst melanistic cordylid populations represent contracting cold-adapted forms.

The aim of the present study was to attempt falsification of the Mouton-Oelofsen hypothesis for evolution in the Cordylus cordylus complex. If it can be demonstrated that isolated melanistic populations of Cordylus polyzonus are not closest relatives but merely ecotypes in a larger gene pool, the evolutionary history of the Cordylus cordylus complex must be seen as largely unique and not explainable by the causes of some more general pattern as proposed by Mouton and Oelofsen (1988). If on the other hand, the isolated melanistic populations of C. polyzonus are more closely related to each other than to non-melanistic populations which separate them geographically, the hypothesis of Mouton and Oelofsen (1988) that the melanistic cordylid populations are relict populations which resulted from the contraction of much larger melanistic populations which prevailed during the Last Glacial, will be partly underscored.

The most obvious way of investigating relationships would be through an analysis of geographic variation in external morphological characters. If the melanistic populations are fragments of a once larger population the chances are good that they might share certain non-adaptive characters that arose through genetic drift in the mother population. Such characters would be good indicators of relationship (Endler 1982). If on the other hand, the melanistic populations are ecotypes in a single gene pool, one would expect clinal trends in adaptive characters and would not expect melanistic populations to share non-adaptive character states.

MATERIALS AND METHODS

Cordylus polyzonus specimens were collected from 93 localities in the region south of $32^{0}15'$ latitude and west of $19^{0}30'$ longitude in the Cape Province (Figure 1). Where sample sizes for localities were too small, neighbouring localities were pooled after a preliminary investigation of character variation was done, as suggested by Sokal (1965). Only localities with expected similar environmental conditions and among which gene flow can occur freely, were pooled.

Character analysis: Variation in 122 external morphological features (Appendix 1), including 43 morphometric, 19 meristic, and 27 qualitative characters, was investigated. In this report only those characters which showed interlocality variation will be discussed, but information on the other characters investigated is available from the authors.

Colour: Although four colour variations of Cordylus polyzonus were identified in the study area, populations were regarded either as melanistic or non-melanistic for the purposes of this study. This differention was easily achieved without the use of any special apparatus.

Loreal-preocular state: In the specimens investigated, the loreal was either fused with the adjacent preocular shield or not (Figure 3a & b). The frequency of occurrence of the fused state (hereafter described as the LP-state) at each locality was presented as a percentage of the total sample size for that locality. Since intra-specimen variation was observed, the left and right sides of each specimen were treated separately to account for such variation. The number of recorded cases accordingly doubled the number of specimens examined.

<u>Median subocular state</u>: Two conditions were observed for the median subocular shield namely bordering the mouth, thereby separating the fourth and fifth upper labials, or not bordering the mouth (Figure 3a & c). The frequency of occurrence of the median subocular not bordering the mouth (hereafter described as the MSnb-state) was expressed as a percentage of the total sample size for each sample locality. Left and right sides were treated separately to account for intra-specimen variation.

<u>Fused subocular state</u>: Although the first and second suboculars were generally separate shields, cases were encountered where they were fused to form a single shield (Figure 3a & d). The frequency of occurrence of this fused state (hereafter referred to as the Sf-state) was recorded for each sample locality and presented as a percentage of the total sample size for that locality. Right and left sides were treated separately for each individual.

<u>Number of femoral pores</u>: Because <u>C</u>. <u>polyzonus</u> females do not posses femoral pores, only counts for male specimens were made. Variation in pore counts between left and right thighs were accounted for by taking a total count for each individual. The mean, standard deviation and range was calculated for each sample locality which included males in the sample.

<u>Snout-vent length</u>: In determining interlocality variation in snout-vent length, all individuals smaller than 75 mm were excluded from the samples. Measurements were taken from the tip of the nose to the cloacal opening. Results were presented as a mean, standard deviation and range for each of the sample localities.

RESULTS

The 93 localities where <u>C</u>. <u>polyzonus</u> has been collected in the south-western Cape, were grouped into 41 compound localities (Appendix 2), (Figure 4) of which localities 1-20 represent melanistic populations and 21-41 non-melanistic ones. Comparing these localities to all the localities visited in the study area (Figure 5), it is evident that this species is well represented on coastal rock, rocky outcrops along the coastal lowlands and on the lower slopes of mountains in the south-western Cape. <u>C</u>. <u>polyzonus</u> was, however, not found at localities south of 34^0 latitude. The absence of these lizards in the north-western part of the study area is due to a large stretch of sandy soil void of any rocky outcrops, which is unsuitable habitat for rupicolous lizards.

The frequency of occurrence of three different headshield character states showing variation in the C. polyzonus complex, is listed in Table 1 and mapped in Figures 6 & 7. It is immediately evident that in general these three character states vary geographically together and that three geographical regions of occurrence can be distinguished, namely a Lamberts Bay-Elands Bay region, a Platberg-Piketberg region and a Saldanha-Langebaan region. The former and the latter include coastal localities at low altitude, while the Platberg-Piketberg region comprises inland localities at relatively high elevation. Furthermore, the two coastal regions of occurrence include all the melanistic C. polyzonus populations in the study-area and also exclusively so (Figure 1). The Platberg-Piketberg region of occurrence, on the other hand, only includes individuals of the brown variation (Figure 1).

In the Lamberts Bay-Elands Bay region all three character states are absent in compound Locality 2, which comprises the eastern inland populations (Figure 4). In the Saldanha-Langebaan region a core area (Localities 7-12) can be distinguished where all three character states occur at the localities. In the rest of the localities either one or two of the character states are absent.

Mean total femoral pore counts, standard deviations and ranges recorded for sample localities containing male specimens, are presented in a modified Dice-Leraas diagram (Figure 8). Although intra-locality variation was generally high and no statistical significant differences were obtained, certain tendencies were observed. The Worcester-Villiersdorp region, with red specimens (Figure 1), and Saldanha-Langebaan region, with melanistic individuals, exhibited the lowest pore counts ranging between 22-27 and 22-28 femoral pores per individual, respectively. Pore counts for turquoise and brown groups ranged between 24-30 and 25-30, respectively. Exceptionally high counts were recorded in localities of the Lamberts Bay-Elands Bay region, with between 26-32 pores per individual. With exception of these localities (1, 2, 3), it appears that lower pore counts are characteristic of populations along the western coastal regions and localities of relatively high altitude along the Cape Fold Mountains, while inland non-melanistic populations generally have higher pore counts.

In Figure 9, mean snout-vent length, standard deviation and range recorded at the sample localities, are depicted in a modified Dice-Leraas diagram. Although an attempt was made to use only adult specimens emphasis should be placed on mean and maximum values only when comparing localities, since minimum values might represent subadult specimens.

From Figure 9 it is evident that melanistic specimens (Localities 1-20) were normally smaller than specimens from non-melanistic localities (Localities 21-41). Comparing mean snout-vent measurements statistically, a significant difference was found between melanistic forms, with an average snout-vent length of 105.6 mm, and non-melanistic forms, with an average snout-vent length of 113.1 mm ($P < 0.001$, $df = 39$). Melanistic specimens never exceeded measurements of 119 mm, while measurements of up to 134 mm were recorded among specimens of the turquoise form. Non-melanistic specimens at localities of relatively high altitude tend to have smaller body sizes, since maximum values recorded for brown and red forms were 122 mm and 117 mm, respectively.

DISCUSSION

The low incidence of the LP, MSnb and Sf-states at the localities where they have been recorded, indicates that these character states are not under strong environmental control. Under such conditions these states would either have been absent in all individuals or present in all individuals. We are therefore of opinion that these three character states are non-adaptive and probably have arisen through genetic drift in a small gene pool. Endler (1982) maintains that good taxonomic characters are supposed to drift as it would reflect the true phylogenetic pattern when not subjected to selection. We accordingly propose that populations from the three regions where these states have been recorded, are from the same stock and therefore genealogically related.

From Figure 1, it is evident that at present the Lamberts Bay-Elands Bay and Platberg-Piketberg populations are geographically separated from the Saldanha-Langebaan population by a stretch of sandy soil. At present gene flow between these populations is only possible via populations of the turquoise variation in the south (Figure 1). None of the three headshield character states occur in these southern populations, suggesting that this route has never been operative.

The obvious explanation for the observed pattern is that some time in the past a larger melanistic population, also displaying the three characteristic headshield states, occurred all along the south-western coastal lowlands, including areas presently occupied by the turquoise, brown and red colour morphs. At some stage, due to changing climatic conditions, this mother population contracted and fragmented with isolated populations remaining only in suitable enclaves. The non-melanistic colour morphs only at a later stage immigrated into the area from more inland areas to occupy areas formerly occupied by the melanistic morphotype.

This view is in agreement with that of Mouton & Oelofsen (1988) for melanistic C. niger and C. oelofseni populations in the same area. Furthermore, Badenhorst & Mouton (under review) established that all coastal melanistic populations occur in association with the upwelling zones in the Atlantic ocean and propose that conditions of lower mean temperatures and a high incidence of advective sea fog associated with these zones, some time in the past, prevailed over most of the regions. Large melanistic cordylid populations occurring along the coastal lowlands fragmented as climates ameliorated to the present situation. This view is underscored by the fact that C. polyzonus individuals from Localities 18, 21 and 22, which represent the nearest points between the Saldanha-Langebaan melanistic population and the turquoise population to the south, not only differ in the non-adaptive characters mentioned above, but there is also a highly significant difference in body size between these forms ($P < 0.001$, $DF = 39$) (Figure 9). The absence of smooth clinal trends indicates that the melanistic and turquoise populations do not belong to the same primary gene pool and that the turquoise morphotype probably at a later stage moved into the area.

Moreover, the situation in the Platberg-Piketberg region, where individuals display the non-adaptive headshield character states, but are non-melanistic, is indicative of swamping of a melanistic population by the brown morphotype rather than a clinal trend in a single gene pool. The Platberg-Piketberg region also supports populations of the melanistic taxa C. oelofseni and Pseudocordylus capensis (Mouton 1987; Mouton & Oelofsen 1988), suggesting that this region could have acted as a sanctuary for a melanistic C. polyzonus population during changing climates. At present, this region being of relative low elevation and falling outside the influence sphere of the Atlantic upwelling zones, melanistic populations, although able to survive there, do probably not have a selective advantage over non-melanistic populations and could easily have been swamped by such populations. Mouton (1987) identified similar populations with intermediate character suites in close proximity to present melanistic populations of C. niger and C. oelofseni and Mouton & Oelofsen (1988) maintain that these populations represent the swamping of melanistic populations of these two species by the expanding non-melanistic species, C. cordylus.

The association of a smaller body size with melanism in C. polyzonus, has also been reported for C. oelofseni (Mouton 1987). Smaller body size is characteristic of ectotherms occupying exposed habitats (Cowles 1941; Cole 1943; Bogert 1949) and the smaller body size of the melanistic C. polyzonus individuals therefore underscores that these individuals are adapted to adverse climatic conditions as proposed by Mouton & Oelofsen (1988). Like coloration, body size is a highly adaptive character trait and one would expect smooth clinal trends in association with gradual changes in the climates. The abrupt change in coloration and body size between the melanistic and turquoise populations in the southern Saldanha-Langebaan region would suggest that if these populations represent ecotypes in a single genepool, there is an abrupt transition in prevailing climatic conditions as well.

The seemingly lower femoral pore counts recorded for coastal populations of C. polyzonus is not in agreement with results obtained by Mouton (1987) for the C. cordylus complex in the same general area. He recorded higher femoral pore counts for the coastal melanistic species C. niger than for the inland species C. cordylus and C. oelofseni. The significance of this difference is at this stage uncertain.

In summary, the results obtained in this analysis do not allow falsification of the Mouton-Oelofsen hypothesis that melanistic cordylid populations are relict populations. In fact, congruency in the geographical distribution of the three non-adaptive headshield characters and the geographical distribution of adaptive characters such as melanism, suggests that melanistic populations of C. polyzonus are remnants of a once larger population. These results should, however, not be seen as conclusive and should be confirmed using other data sets as well.

Although Mouton and Van Wyk (1990) elevated the two melanistic morphotypes in the Cordylus cordylus complex to full species, it would at this stage be premature to come to any conclusions regarding the taxonomic status of the melanistic morphotype of C. polyzonus. In the present study only melanistic populations of this species south of $32^{0}15'$ latitude were included in the analysis. Melanistic populations have, however, also been reported from several other localities along the west coast as far as the Orange River in the north and the analysis should be extended to include these as well. This would, however, mean that an extensive distribution survey would have to be done to account for all geographic variation in this species along the western coastal regions. Only then would it be possible to discuss the taxonomic status of the melanistic morphotype of C. polyzonus.

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Table 1 Frequency of occurrence (5) of the three head shield characters showing variation among 41 compound localities in the study area. LP - loreal and preocular fused; MSnb = median subocular not bordering the mouth; Sf = first and second subocular fused; N = sample size.

Locality	N	LP	MSnb	Sf
1	11	9	18	0
2	9	0	0	0
3	8	6	0	6
4	10	0	45	0
5	7	14	14	0
6	6	0	17	0
7	11	9	32	5
8	4	13	37	13
9	11	18	50	9
10	5	30	40	10
11	9	17	77	11
12	20	10	60	3
13	12	29	42	0
14	12	46	12	0
15	6	75	33	0
16	6	67	42	0
17	8	75	25	0
18	7	79	0	0
19	11	9	27	0
20	7	0	50	0
21	13	0	0	0
22	8	0	0	0
23	6	0	0	0
24	10	0	0	0
25	6	0	0	0
26	5	0	0	0
27	7	0	0	0
28	8	0	0	0
29	5	20	20	0
30	6	0	25	17
31	4	0	75	0
32	2	0	0	0
33	12	17	8	8
34	7	0	100	7
35	4	0	25	0
36	7	0	0	0
37	6	0	0	0
38	4	0	0	0
39	3	0	0	0
40	4	0	0	0
41	5	0	0	0
Total	306			

LIST OF FIGURES

Figure 1. Distribution patterns of the different colour morphs of the Cordylus polyzonus complex in the south-western Cape.

Figure 2. Distribution patterns of the taxa of the Cordylus cordylus complex in the south-western Cape.

Figure 3. Lateral view of the head of Cordylus polyzonus showing: (a) the loreal and preocular not fused; the median subocular bordering the mouth; the first and second suboculars not fused. (b) the loreal and preocular fused. (c) the median subocular not bordering the mouth. (d) the first and second suboculars fused.

Figure 4. Distribution of the compound localities at which Cordylus polyzonus occur in the study-area.

Figure 5. Localities visited in the study-area.

Figure 6. Contour map showing the geographic distribution of frequencies of occurrence of the LP and MSnb character states for C. polyzonus populations in the study-area.

Figure 7. Contour map showing the geographic distribution of frequencies of occurrence of the Sf character state C. polyzonus populations in the study-area.

Figure 8. A modified Dice-Leraas diagram of the mean femoral pore counts of male C. polyzonus individuals (vertical line), standard deviations (solid bars) and the ranges (horizontal lines) recorded at 39 localities in the study-area. Locality number appears on the left and sample size on the right.

Figure 9. A modified Dice-Leraas diagram of the mean snout-vent lengths (vertical lines), standard deviations (solid bars) and the ranges (horizontal lines) recorded for C. polyzonus individuals at 41 localities in the study-area. Locality number is given on the left and sample size on the right.

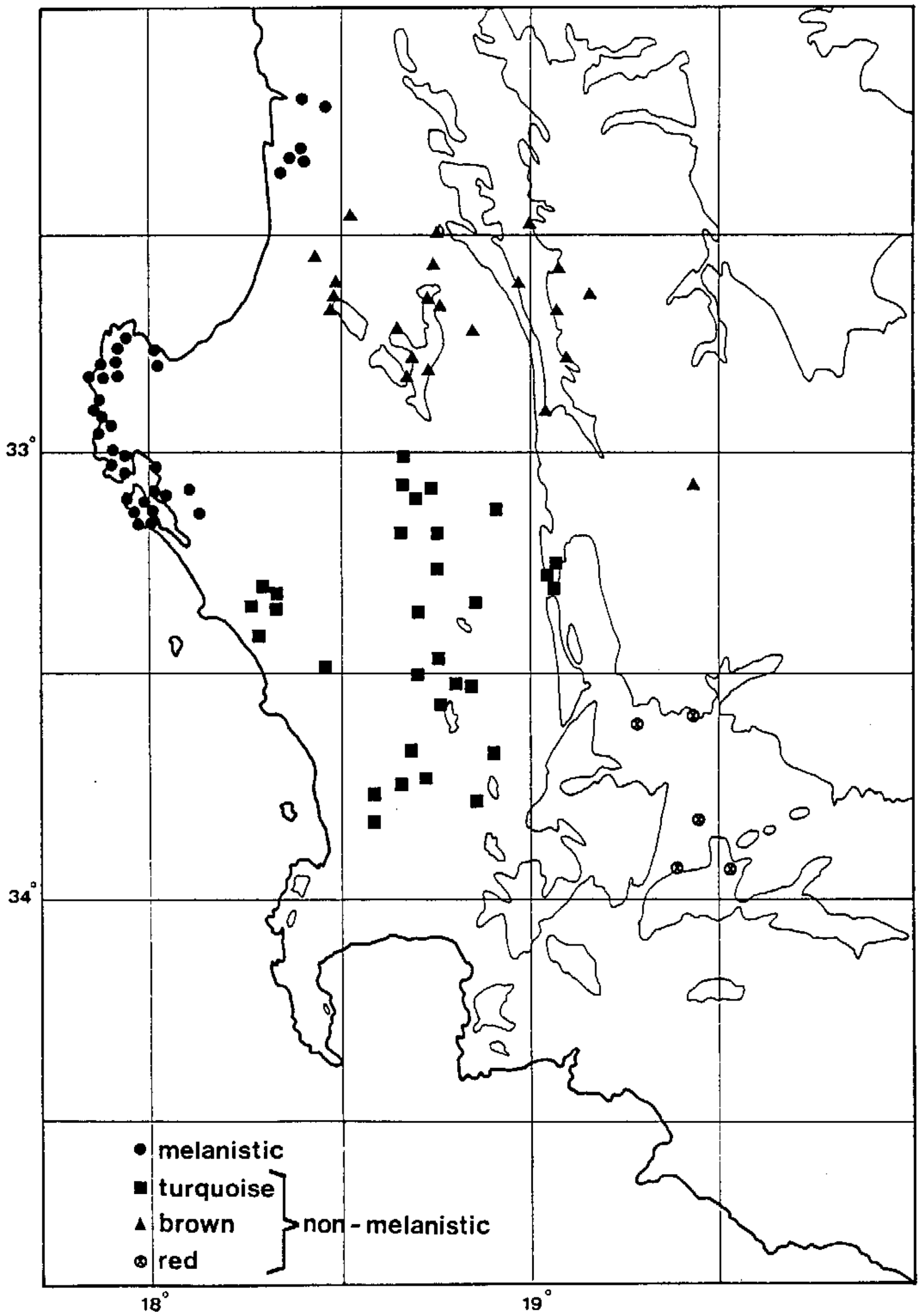

Figure 1

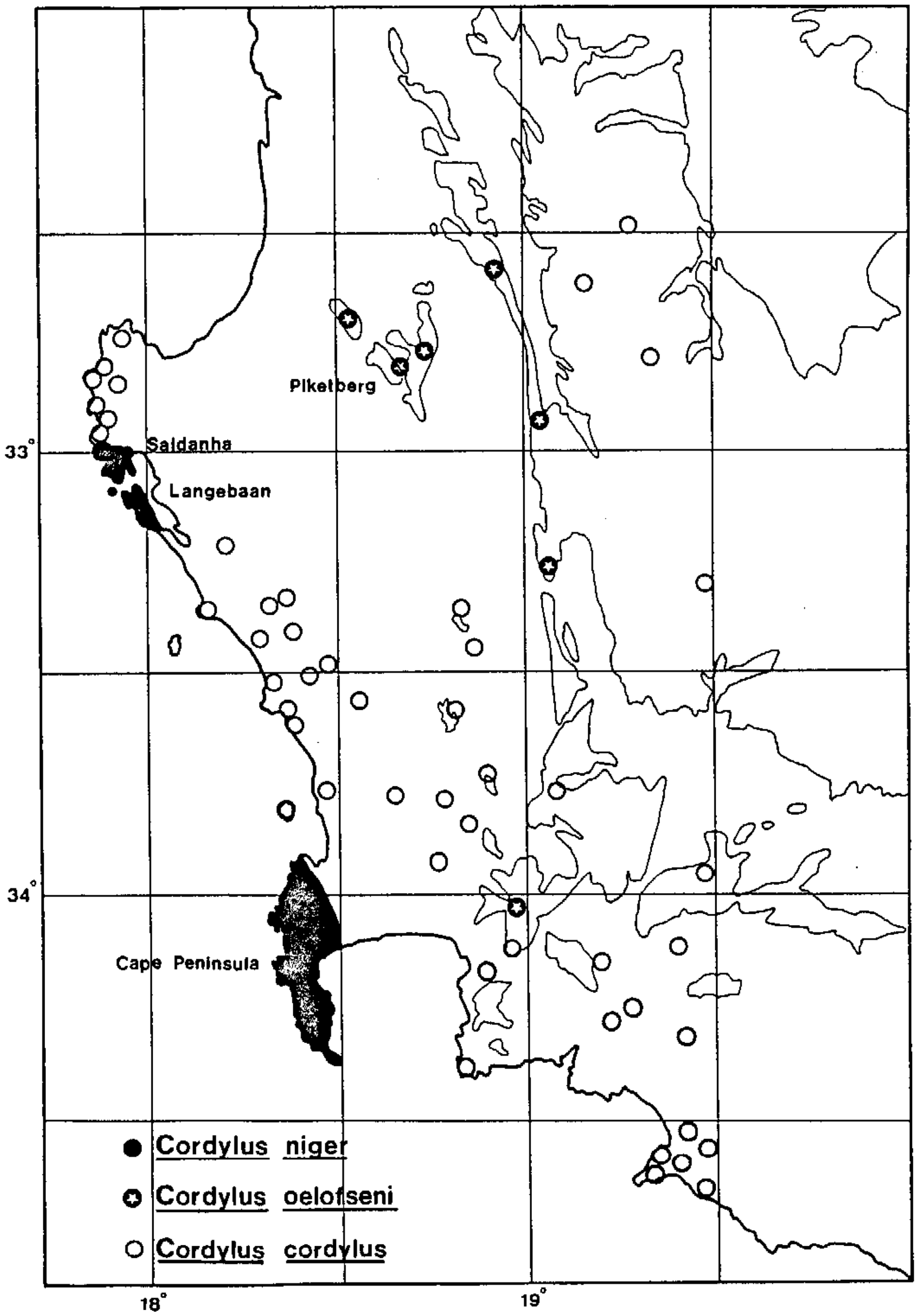
Piketberg
Saldanha
Langebaan
Cape Peninsula
33°
34°
18°
19°
Cordylus niger
Cordylus oelofseni
Cordylus cordylus

Figure 2.

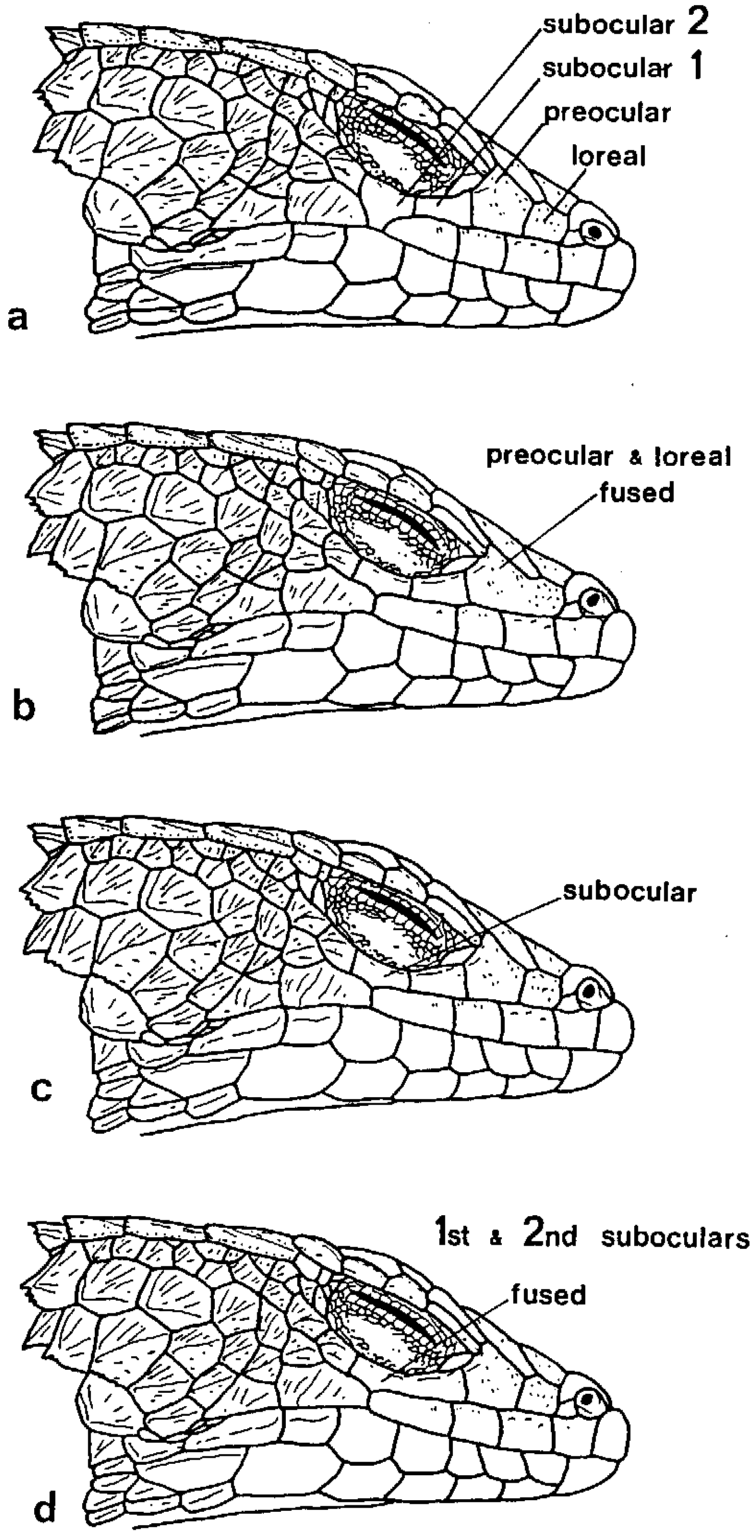
subocular 2
subocular 1
preocular
loreal
a
preocular & loreal
fused
b
subocular
c
1st & 2nd suboculars
fused
d

Figure 3.

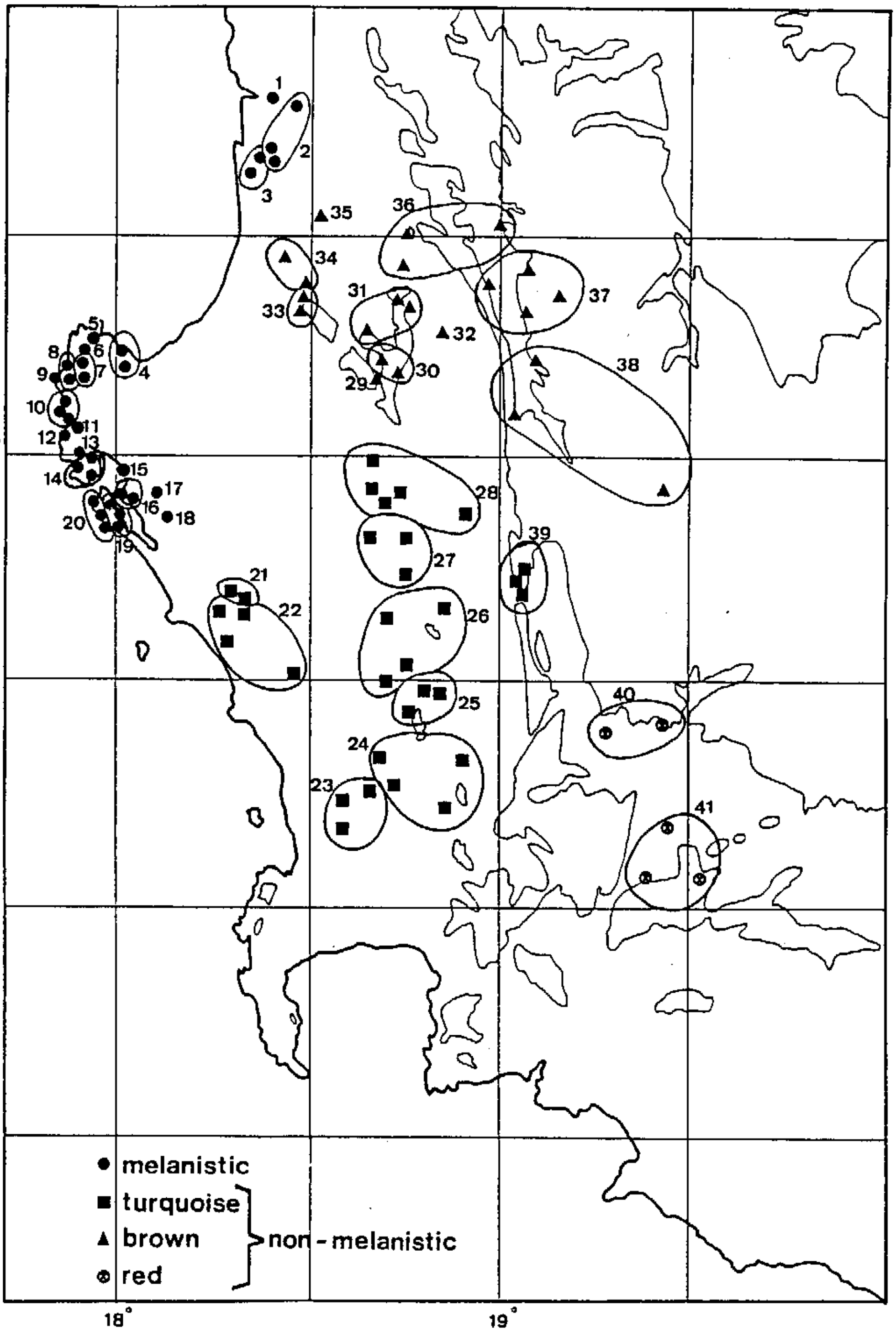
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
33°
34°
18°
19°
melanistic
turquoise
brown
red
non-melanistic

Figure 4.

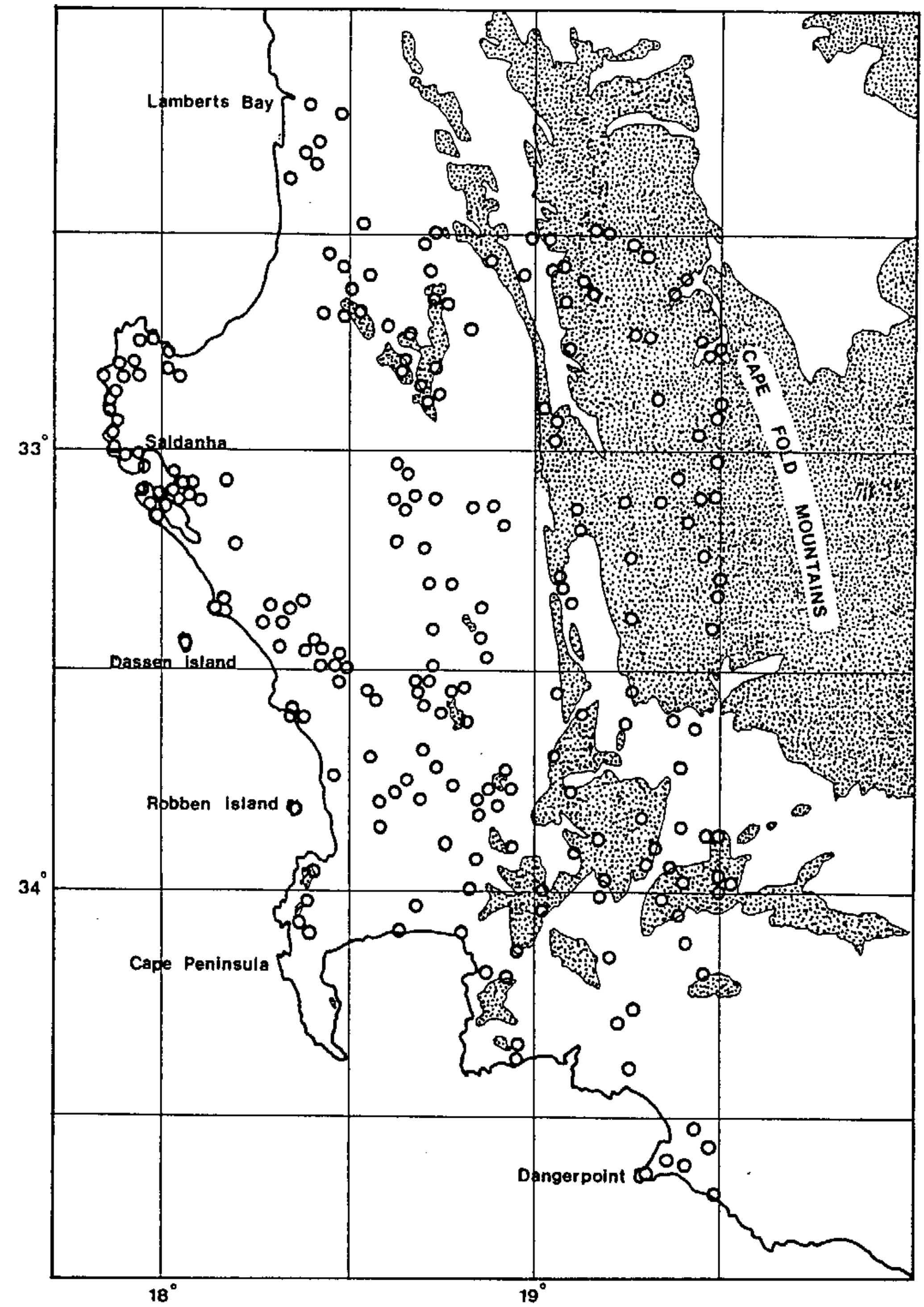
Lamberts Bay
Saldanha
Dassen Island
Robben Island
Cape Peninsula
Dangerpoint
CAPE FOLD MOUNTAINS
33°
34°
18°
19°

Figure 5.

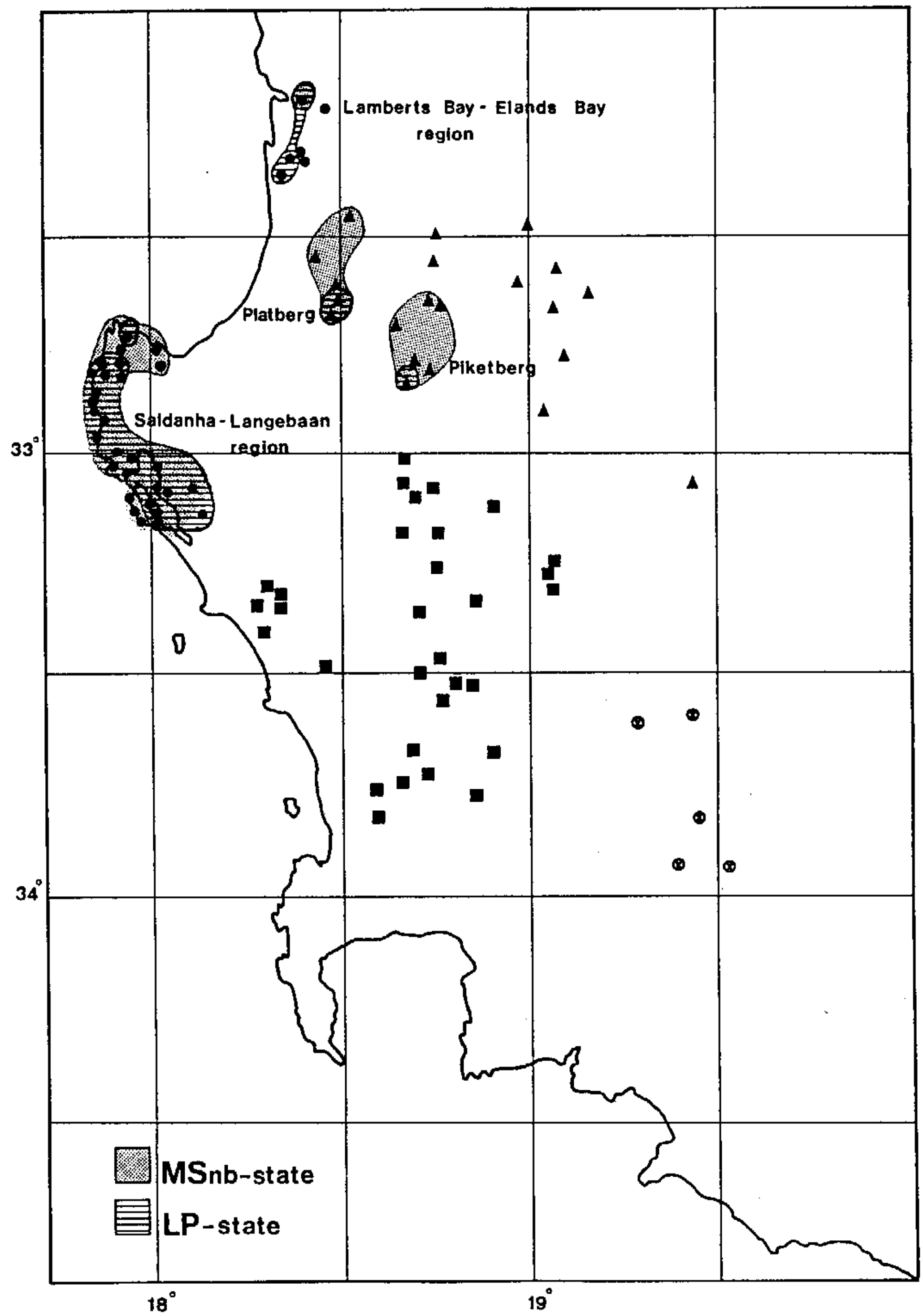
Lamberts Bay - Elands Bay
region
Platberg
Piketberg
Saldanha - Langebaan
region
33°
34°
18°
19°
MSnb-state
LP-state

Figure 6.

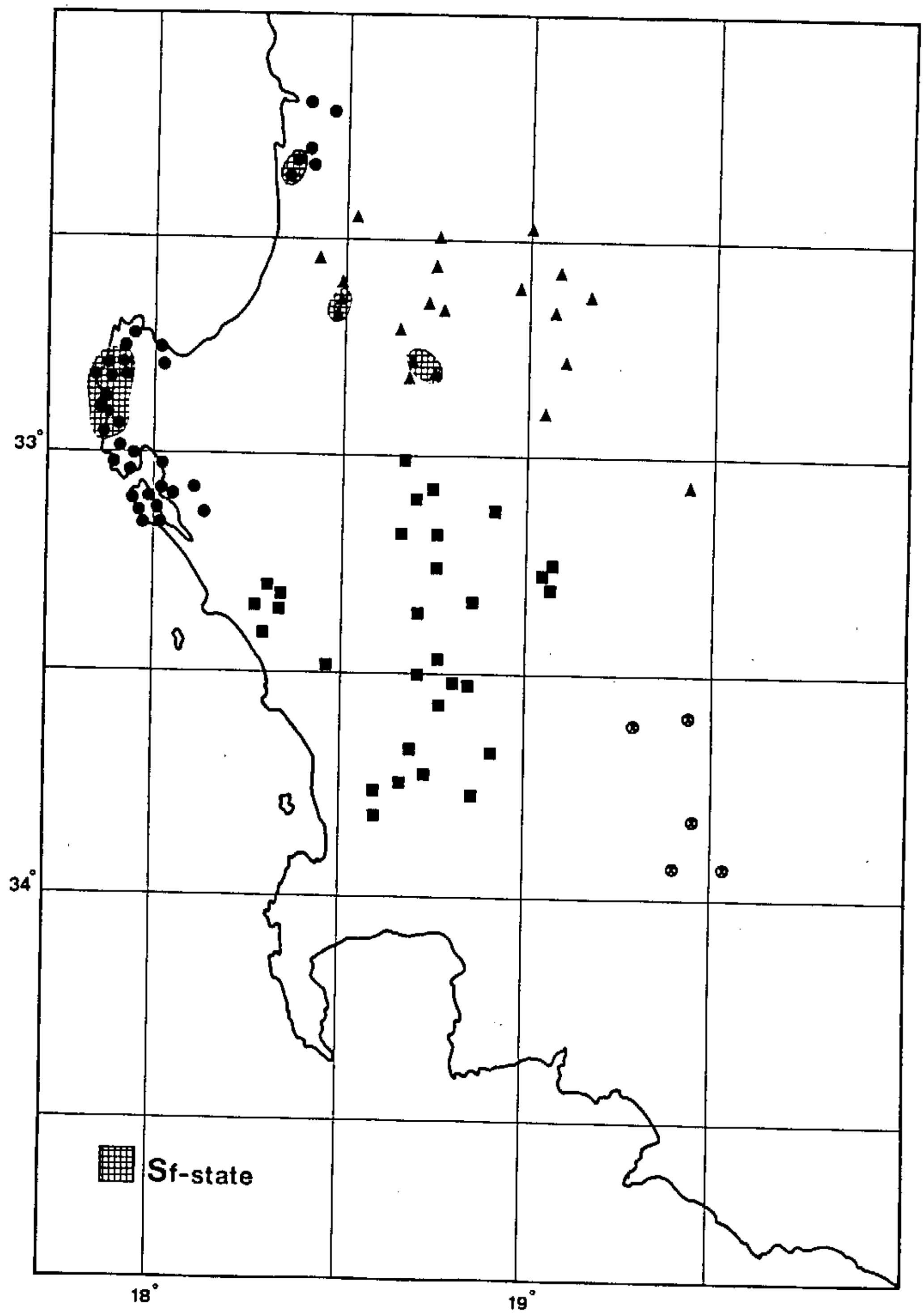

Figure 7.

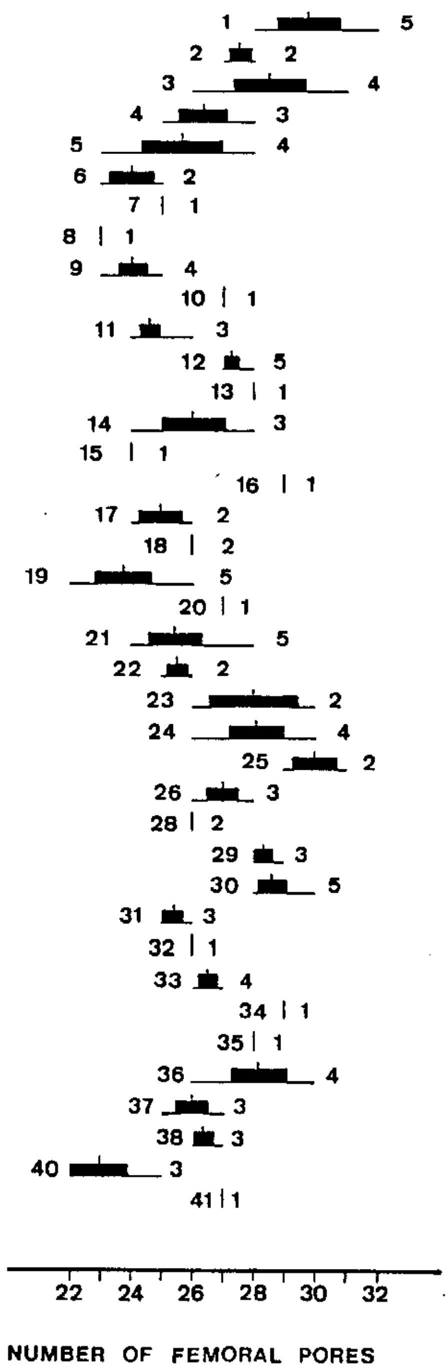

Figure 8.

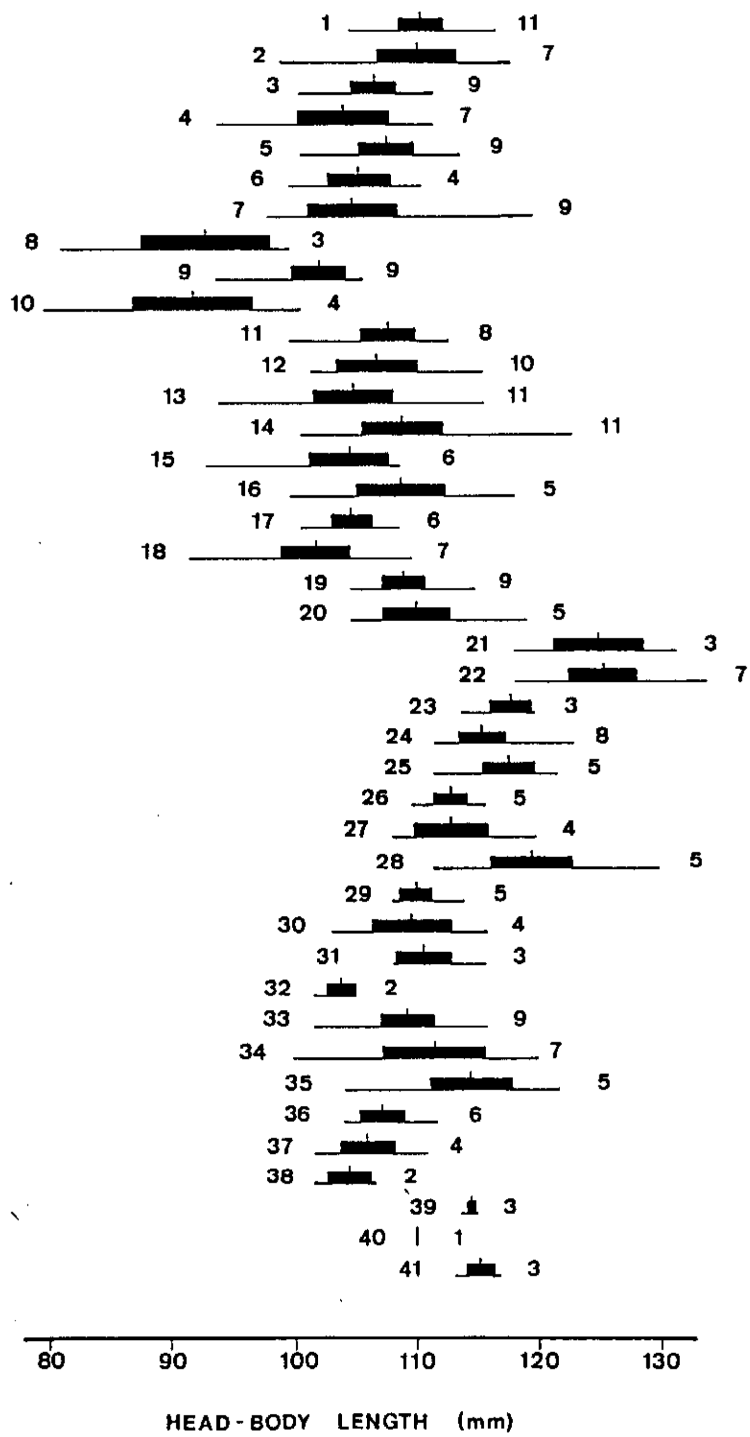
1 11
2 7
3 9
4 7
5 9
6 4
7 9
8 3
9 9
10 4
11 8
12 10
13 11
14 11
15 6
16 5
17 6
18 7
19 9
20 5
21 3
22 7
23 3
24 8
25 5
26 5
27 4
28 5
29 5
30 4
31 3
32 2
33 9
34 7
35 5
36 6
37 4
38 2
39 3
40 1
41 3
80
90
100
110
120
130
HEAD-BODY LENGTH (mm)

Figure 9.

APPENDIX 1: List of external morphological characters used for the analysis of phenotypic character variation in the Cordylus polyzonus complex.

A. Morphometric characters

1. Length of head
2. Breadth of head
3. Depth of head
4. Breadth of rostral
5. Depth of rostral
6. Length of supranasal at suture
7. Breadth of supranasal at suture
8. Length of frontonasal
9. Breadth of frontonasal
10. Length of prefrontal at suture
11. Breadth of prefrontal
12. Lenght of frontal
13. Breadth of frontal
14. Length of frontoparietals
15. Breadth of frontoparietals
16. Length of anterior parietals
17. Breadth of anterior parietals
18. Length of posterior parietals
19. Breadth of posterior parietals
20. Length of interparietal
21. Breadth of interparietal
22. Length of anterior temporal
23. Breadth of anterior temporal
24. Length of posterior temporal
25. Breadth of posterior temporal
26. Height of eyebrow

27. Breadth of eyebrow
28. Length of eyecase
29. Breadth of eyecase
30. Nuchal diameter
31. Breadth of mental
32. Depth of mental
33. Length of mouth
34. Length of neck
35. Breadth of neck
36. Depth of neck
37. Distance between front and rear legs
38. Distance between front legs
39. Distance between rear legs
40. Snout-vent length
41. Breadth of vent
42. Length of hindlimbs
43. Breadth of forelimbs

B. Meristic characters

1. Number of supracilliaries
2. Number occipitals
3. Number postoccipitals
4. Number scales in row behind postoccipitals
5. Number suboculars
6. Number supraoculars
7. Number upper labials
8. Number upper labials in front of 2nd subocular
9. Number lower labials
10. Number sublabials
11. Number scales between posterior sublabials

12. Number dorsal scales longitudinal
13. Number ventral scales longitudinal
14. Number transverse dorsal scales
15. Number transverse ventral scales
16. Number femoral pores
17. Number lamellae under 4th toe
18. Number lamellae under 4th finger
19. Number of whorls in tail

C. Qualitative characters

1. Loreal fused with preocular or not
2. Suboculars fused or not
3. Second subocular reaching the lip or not
4. Form of frontonasal
5. Frontonasal broader than long or not
6. Supranasals in median contact
7. Form of nasals
8. Direction in which nostrils open
9. Prefrontals in median contact or not
10. Form of frontal
11. Frontal broader anteriorly than posteriorly or not
12. Form of interparietal
13. Anterior parietals smaller than posterior ones or not
14. Temporals strongly keeled or spinose behind
15. Nature of dorsal head shields
16. Nature of ventral head shields
17. Nature of chin scales
18. Position of nuchal
19. Position of central postoccipital
20. Nature of ventral neck scales

21. Nature of scales on lateral sides of neck
22. Nature of dorsal body scales
23. Nature of ventral body scales
24. Nature of lateral body scales
25. Nature of dorsal scales on tail
26. Nature of ventral scales on tail
27. Black strip on side of neck or not

APPENDIX 2: List of the localities and compound localities where Cordylus polyzonus specimens were collected in the study area.

1. Wadrif: 321230S/182300E. 3218 AB Lambert's Bay.

   JEFB 1824-1834; 22.09.1989.

2. Langvleiberge: 321330S/182800E. 3218 AB Lambert's Bay.

   JEFB 1808; 21.09.1989.

   Slangkop: 321818S/182400E. 3218 AD Elands Bay.

   JEFB 1838; 21.09.1989.

   Verlorenvlei: 321936S/182308E. 3218 AD Elands Bay.

   JEFB 1625-1630; 23.02.1988.

3. Skietkop: 321935S/182343E. 3218 AD Elands Bay.

   JEFB 1809-1815, 1899; 21.09.1989.

   Ribbokplaat: 322018S/182006E. 3218 AD Elands Bay.

   JEFB 407; 08.12.1983.

4. Brandhuis: 324607S/180241E. 3218 CA + CC Velddrif.

   JEFB 1638; 24.02.1988.

   Elandskloof: 324655S/180254E. 3218 CA + CC Velddrif.

   JEFB 1631, 1632, 1634-1637; 24.02.1988.

5. Sandy Point: 324443S/180011E. 3218 CA + CC Velddrif.

   JEFB 1639-1641; 24.02.1988.

   JEFB 1862-1868; 10.11.1989.

6. Soetlandskop: 324416S/175723E. 3217 DB & DD Vredenburg.

   JEFB 381, 382; 08.12.1983.

   JEFB 1872-1875; 10.11.1989.

7. Katzenberg: 325027S/175656E. 3217 DB + DD Vredenburg.

   JEFB 531, 532; 02.04.1984.

   Kasteelberg: 324900S/175638E. 3217 DB + DD Vredenburg.

   JEFB 528, 529; 02.04.1984.

   JEFB 1642-1648; 24.02.1988.

8. Pelgrimsrust: 324924S/175358E. 3217 DB + DD Vredenburg.

JEFB 536, 537; 04.04.1984.

Hoedklip: 324945S/175107E. 3217 DB + DD Vredenburg.

JEFB 508, 509; 31.03.1984.

9. Cape Castle: 325000S/175107E. 3217 DB + DD Vredenburg.

JEFB 507; 31.03.1984.

JEFB 1649-1652; 25.02.1988.

JEFB 1856-1861; 11.11.1989.

10. Trekoskraal: 325313S/175356E. 3217 DB + DD Vredenburg.

JEFB 374; 07.12.1983.

Duminypunt: 325334S/175200E. 3217 DB + DD Vredenburg.

JEFB 369, 370; 07.12.1983.

Sandbaai: 325357S/175206E. 3217 DB + DD Vredenburg.

JEFB 362, 363; 07.12.1983.

11. Swartriet: 325739S/175356E. 3217 DB + DD Vredenburg.

JEFB 522-524; 01.04.1984.

JEFB 1664-1669; 26.02.1988.

12. Jacobsbaai: 325752S/175250E. 3217 DB + DD Vredenburg.

JEFB 344; 05.12.1983.

JEFB 1659-1663; 25.02.1988.

JEFB 1839-1843, 1905, 1914-1921; 12.11.1989.

13. Saldanha A: 330005S/175615E. 3317 BB + 3318 AA Saldanha.

JEFB 87-90; 06.04.1983.

JEFB 1845-1852; 11.11.1989.

14. Hoedjieskop: 330040S/175648E. 3317 BB + 3318 AA

Saldanha. JEFB 298, 299; 05.12.1983.

JEFB 1896, 1897; 11.11.1989.

Môresonkop: 330129S/175531E. 3317 BB + 3318 AA Saldanha.

JEFB 339, 340; 05.12.1983.

Malgaskop: 330200S/175837E. 3317 BB + 3318 AA Saldanha.

JEFB 308, 309; 05.12.1983.

JEFB 1890-1893; 11.11.1989.

15. Leentjiesklip B: 330242S/180213E. 3317 BB + 3318 AA

Saldanha. JEFB 284, 285; 04.12.1983.

JEFB 1670-1675; 27.02.1988.

16. Langebaan: 330506S/180300E. 3317 BB + 3318 AA Saldanha.

JEFB 646; 26.05.1984.

JEFB 1678-1680; 27.02.1988.

Meeuklip: 330532S/180337E. 3317 BB + 3318 AA Saldanha.

JEFB 280, 281; 04.12.1983.

17. Karnberg: 330411S/180556E. 3317 BB + 3318 AA Saldanha.

JEFB 276, 277; 03.12.1983.

JEFB 1681-1686; 01.03.1988.

18. Massenberg: 330705S/180806E. 3317 BB + 3318 AA Saldanha.

JEFB 270, 271; 03.12.1983.

JEFB 1687-1691; 01.03.1988.

19. Postberg: 330646S/180018E. 3317 BB + 3318 AA Saldanha.

JEFB 218; 01.12.1983.

Konstabelberg: 330753S/180116E. 3317 BB + 3318 AA

Saldanha. JEFB 265, 266; 01.12.1983.

JEFB 1876-1880; 10.11.1989.

Oude Post: 330700S/180030E. 3317 BB + 3318 AA Saldanha.

JEFB 1853-1855; 11.11.1989.

20. Kreeftebaaikop A: 330812S/175839E. 3317 BB + 3318 AA

Saldanha. JEFB 231; 01.12.1983.

JEFB 1887, 1888; 11.11.1989.

Kreeftebaaikop B: 330825S/175922E. 3317 BB + 3318 AA

Saldanha. JEFB 257; 01.12.1983.

Plankiesbaai: 330754S/175822E. 3317 BB + 3318 AA
Saldanha. JEFB 240-242; 01.12.1988.

21. Turksvyberg: 331945S/181830E. 3318 AD Darling.
JEFB 1901, 1903, 1904, 1906-1913; 12.11.1989.
Klipberg: 332000S/181756E. 3318 AD Darling.
JEFB 424, 425; 12.12.1983.

22. Grootwater B: 332142S/181640E. 3318 AD Darling.
JEFB 641, 642; 26.05.1984.
Bonteberg: 332121S/182015E. 3318 AD Darling.
JEFB 666, 667; 27.05.1984.
Rondeberg: 332518S/181750E. 3318 AD Darling.
JEFB 102, 103; 20.08.1983.
Bobbejaanberg: 332910S/182706E. 3318 AD Darling.
JEFB 91, 92; 16.04.1983.

23. Hoogkraal: 334709S/183437E. 3318 DC Belville.
JEFB 152, 153; 17.09.1983.
Klein Roosboom: 334959S/183426E. 3318 DC Belville.
JEFB 187, 217; 15.10.1983.
Rondebossieberg: 334550S/184000E. 3318 DC Belville.
JEFB 142,143; 17.09.1983.

24. Klipheuwelplaas: 334213S/184143E. 3318 DA Philadelphia.
JEFB 123; 06.08.1983.
JEFB 1869-1871; 10.11.1989.
Kliprug: 334336S/184356E. 3318 DA Philadelphia.
JEFB 94, 95; 17.07.1983.
Wolfieskop: 334635S/185131E. 3318 DD Stellenbosch.
JEFB 489, 490; 13.03.1984.
De Hoop: 334136S/185427E. 3318 DB Paarl.
JEFB 199, 200; 16.10.1983.

25. Doornkraal: 333422S/184329E. 3318 DA Philadelphia.

JEFB 746, 747; 11.07.1984.

Joubertskloof: 333227S/184714E. 3318 DB Paarl.

JEFB 752, 753; 11.07.1984.

Besemgoedkop: 333237S/184813E. 3318 DB Paarl.

JEFB 159, 160; 18.09.1983.

26. Middelpos: 333015S/184241E. 3318 DA Philadelphia.

JEFB 215; 06.08.1983.

Malmesbury: 332843S/184459E. 3318 BC Malmesbury.

JEFB 93; 16.07.1983.

Saamstaan: 332257S/184227E. 3318 BC Malmesbury.

JEFB 787, 788; 04.08.1984.

Voorspoed: 332014S/184927E. 3318 BD Riebeeck-Kasteel.

JEFB 181; 28.09.1983.

27. Kanonberg: 331605S/184452E. 3318 BC Malmesbury.

JEFB 689, 690; 09.06.1984.

Tontelberg: 331131S/184440E. 3318 BA Moorreesburg.

JEFB 695,1330; 09.06.1984.

Neulfontein: 331108S/183956E. 3318 BA Moorreesburg.

JEFB 697, 698, 699; 09.06.1984.

28. Goudmyn se Berg: 330753S/184129E. 3318 BA Moorreesburg.

JEFB 169, 170; 27.09.1983.

Oshoekkop: 330506S/184048E. 3318 BA Moorreesburg.

JEFB 807; 05.08.1984.

Rusoord: 330545S/184402E. 3318 BA Moorreesburg.

JEFB 799, 800; 05.08.1984.

Koringberg: 330052S/183842E. 3318 BA Moorreesburg.

JEFB 701, 702; 10.06.1984.

Heuningberg: 330739S/185325E. 3318 BB Porterville.

JEFB 175; 27.09.1983.

29. Goedverwacht: 325220S/184025E. 3218 DC Moravia.

JEFB 216; 19.11.1983.

JEFB 1881-1884; 10.11.1989.

30. Perdekop: 324757S/183809E. 3218 DA Goergap.

JEFB 471, 472; 19.02.1984.

Koggelmanderkop: 324808S/184237E. 3218 DC Moravia.

JEFB 211, 212; 19.11.1983.

JEFB 1894, 1895; 10.11.1989.

31. Tierhoek: 324730S/183910E. 3218 DC Moravia.

JEFB 1885, 1886; 10.11.1989.

Banghoek: 324334S/183829E. 3218 DA Goergap.

JEFB 831; 19.08.1984.

Keurbosberg: 323942S/184431E. 3218 DB Eendekuil.

JEFB 820; 18.08.1984.

32. Union: 324308S/184856E. 3218 DB Eendekuil.

JEFB 793, 794; 04.08.1984.

33. Soetgoedkop: 324145S/182854E. 3218 CB & CA Aurora.

JEFB 1793-1799; 20.09.1989.

Platberg: 324024S/182707E. 3218 CA + CB Aurora.

JEFB 1574-1578; 23.09.1986.

34. Rietvlei: 323711S/182938E. 3218 CA + CB Aurora.

JEFB 418, 419; 11.12.1983.

Klein Tafelberg: 323308S/182750E. 3218 CA + CB Aurora.

JEFB 841; 01.09.1984.

JEFB 1835-1837, 1900; 22.09.1989.

35. Kalmberg: 322735S/183156E. 3218 BC Redelinghuys.

JEFB 1800-1803, 1902; 20.09.1989.

36. Bruinkrans: 323403S/184342E. 3218 DB Eendekuil.

JEFB 823, 824; 18.08.1984.

Waterberg: 323016S/184302E. 3218 DA Goergap.

JEFB 760-762; 14.07.1984.

Brakfontein: 322932S/190037E. 3219 AC Wuppertal.

JEFB 768, 769; 15.07.1984.

37. Spitskop: 323413S/190313E. 3219 CA Citrusdal.

JEFB 1232, 1233; 10.08.1985.

Piekenierskloof: 323721S/185733E. 3218 DB Eendekuil.

JEFB 1071; 10.03.1985.

Fairview: 323909S/190450E. 3219 CA Citrusdal.

JEFB 1382, 1383; 01.02.1985.

Middelbergpas: 323753S/190906E. 3219 CA Citrusdal.

JEFB 1156; 26.05.1985.

38. Dasklippas: 325425S/190214E. 3219 CC Keerom.

JEFB 947; 19.12.1984.

Goudinikop: 324711S/190554E. 3219 CC Keerom.

JEFB 1225, 1226; 10.08.1985.

Loch Lynnne: 330523S/192629E. 3319 AB Gydopas.

JEFB 1130; 12.05.1985.

39. Nuwekloofpas: 331847S/190437E. 3319 AC Tulbach.

JEFB 949; 19.12.1984.

Obiekwa A: 331558S/190407E. 3319 AC Tulbach.

JEFB 966; 26.01.1985.

Obiekwa B: 331616S/190352E. 3319 AC Tulbach.

JEFB 969; 26.01.1985.

40. Die Nekkies: 334122S/191506E. 3319 CB Worcester.

JEFB 911-913; 28.10.1984.

Die Ruimte: 333645S/192506E. 3319 CB Worcester.

JEFB 909; 28.10.1984.

41. Lemoenkloof B: 335119S/192819E. 3319 CD Villiersdorp.

JEFB 1255; 18.08.1985.

Kleinfontein: 335627S/192342E. 3319 CD Villiersdorp.

JEFB 1265, 1267; 01.09.1985.

Suurberge: 335631S/193123E. 3319 DC Langvlei.

JEFB 881, 882; 29.09.1984.

CLIMATES ASSOCIATED WITH THE EVOLUTION OF MELANISM IN CORDYLID LIZARDS IN THE SOUTH-WESTERN CAPE, SOUTH AFRICA

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Prevailing climatic conditions associated with the occurrence of melanistic populations of the lizard genera Cordylus and Pseudocordylus in the south-western Cape, have been investigated. Coastal melanistic populations occur on islands in or on the mainland adjacent to upwelling zones of cold water in the Atlantic ocean. Climatic conditions associated with these zones are lower mean daily temperatures and a high incidence of advective sea fog. Inland melanistic populations occur at relatively high altitudes also associated with lower mean daily temperatures and a high incidence of orographic fog or cloud cover. It is postulated that the entire western coastal region, at least as far as the Orange River, was subjected to similar conditions during the Last Glacial Period, conditions which were instrumental in the evolution of melanistic cordylid taxa during this time.

Huidige klimaatstoestande geassosieer met die voorkoms van melanistiese populasies van die genera Cordylus en Pseudocordylus in die suidwes-Kaap is ondersoek. Langs die kus kom melanistiese populasies voor op eilande in, of op die vasteland teenoor opwellingsones van koue water in die Atlantiese oseaan. Klimaatstoestande geassosieer met hierdie sones is laer gemiddelde dagtemperature en 'n hoë voorkoms van mis. Binnelandse melanistiese populasies kom relatief hoog in die berge voor waar soortgelyke toestande van laer gemiddelde dagtemperature en 'n hoë voorkoms van orografiese mis of wolkbedekking heers. Daar word voorgestel dat gedurende die Laaste Ystydperk, soortgelyke toestande oor die hele westelike kusgebiede voorgekom het, ten minste so ver

noord as die Oranjerivier, en dat hierdie toestande betrokke was by die evolusie van melanistiese akkedistaksa gedurende hierdie tyd.

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INTRODUCTION

Two main hypotheses have been advanced to account for the colours of lizards and many other animals, although some species may possess colours with little or no advantage to survival. In species subject to predation colour may provide protection from predators through background colour-matching (cryptic coloration), countershading, patternmatching, warning colours and mimicry (Norris 1967; Porter 1972; Endler 1978; Hoppe 1979). Different colorations also affect heat balance through the differential reflection and absorption of incident radiation (Porter 1972; Gibson & Falls 1979; Hoppe 1979). Beside these two important functions of colour it is also often involved in sexual displays, in species and sex recognition, and in interactions between different species (Porter 1972). Colour also functions to provide radiation shields for critical structures and organs (Hunsaker & Johnson 1959; Porter 1967).

Although melanism in reptiles has been reported worldwide (Petzold 1972; Malkmus 1976; Mitteilungen 1978; Crisp, Cook & Hereward 1979; Gibson & Falls 1979; Worsnip 1980), few attempts have been made to interpret the functional and historical importance of this phenomenon. Mouton (1986a), however, mapped the distribution of melanistic lizards of the subfamily Cordylinae in southern Africa and established that, with the exception of a melanistic population of Cordylus polyzonus in the north-eastern Cape and southern Orange Free State, these melanistic cordylids are restricted to the south-western coastal regions of the Cape Province. Melanistic taxa in this region include Cordylus peersi, Cordylus niger, Cordylus oelofseni (sp. nov., Mouton & van Wyk 1990), Cordylus coeruleopunctatus, Cordylus polyzonus and Pseudocordylus capensis. Cordylus polyzonus is a polymorphic species which comprises both melanistic and non-melanistic colourmorphs, while the other five species are exclusively melanistic.

Invariably the melanistic taxa in the south-western Cape occur in the form of small, isolated populations, which, in the case of Cordylus polyzonus, might geographically be separated by populations of non-melanistic morphotypes. The present restricted distribution of melanistic forms and the fact that Cordylus niger and Cordylus oelofseni share several non-adaptive characters although they are geographically separated by a closely related species, Cordylus cordylus, led Mouton & Oelofsen (1988) to conclude that large melanistic populations occurred in the south-western Cape some time in the past. These they maintain, became fragmented during climatic changes along the south-western coastal areas. They accordingly see the present melanistic populations as relict populations which survived in suitable refugia.

Badenhorst, Mouton & Van Wyk (under review) established that melanistic populations of the polymorphic species, Cordylus polyzonus, share several non-adaptive characters and are probably genealogically related, although they are geographically separated by populations of a conspecific non-melanistic colourmorph. Their findings underscore the conclusions of Mouton & Oelofsen (1988) that, in general, the melanistic cordylid populations in the south-western Cape are relict populations and that closely related non-melanistic forms, which today separate melanistic populations, are newcomers to the south-western Cape, having only recently immigrated into the area from more inland regions.

Moreover, Mouton & Oelofsen (1988) maintain that the concentration of melanistic taxa along the south-western coastal areas, as well as the peculiar distribution of the melanistic populations in these areas, in insular and peninsular situations along the coast and at higher altitudes inland (Figure 1), indicate that melanism evolved in response to certain climatic pressures rather than biotic or other factors. In the light of the thermoregulatory advantages of a dark skin in cold environments (Norris 1967; Porter 1967; Heatwole 1976; Pearson 1977; Rice & Bradshaw 1980), they postulated that melanism in the taxa under question evolved during the Last Glacial Period in response to adverse climatic conditions. Furthermore, they advocate that during the Last Glacial the influence of the Cold Benguela Current on the climates of the south-western coastal regions was more pronounced than at present and, in fact, that the effects of the Benguela Current and associated upwelling system are primarily responsible for the high incidence of melanistic cordylid populations along coastal regions.

It is today generally accepted that all organisms are persistent in environmental conditions to which they have adapted during their speciation (Vrba 1985; Endrödy-Younga 1988). Knowledge of the climatic conditions which prevail at those localities where melanistic populations occur today, would provide some perspective of those conditions which must have prevailed at a grand scale along the south-western coastal regions at the time melanism evolved in cordylid lizards in this area. The aim of the present study accordingly was to characterize the climatic regimes associated with the occurrence of extant melanistic cordylid populations. Not only will such information provide insight into the palaeoclimates of the south-western Cape, but will also elucidate the functional significance of melanism. Moreover, the study will provide the opportunity to investigate the claims of Mouton & Oelofsen (1988) that melanistic cordylid populations represent "cold-adapted" forms.

MATERIALS AND METHODS

The area south of 32^{0}15' latitude and west of 19^{0}15' longitude was selected as study-area because of the availability of climatic data for this region, as well as extensive distributional data for the four melanistic species occurring in the area. The distributional data for the four taxa (Figure 1) come from a survey done over a period of four years during which time more than 250 localities were visited in the study-area. Climatic data were obtained from 123 weather stations in the study-area (Figure 2; Appendix 1). For most stations the data are representative of a period of 10 or more consecutive years. Mean annual daily temperatures (recorded at 117 stations) and mean annual sunshine hours per day (recorded at 56 stations) were calculated. The incidence of advective sea fog, obtained from 30 stations, was expressed as a percentage of days per year with fog. Other relevant data were obtained from the literature.

RESULTS AND DISCUSSION

The study-area comprises a wide variety of habitats owing to the heterogenous topography and bathymetry. In the west, the coastal regions are subjected to the strong influence of the northflowing Cold Benguela Current (Figure 2). This coastal strip is renowned for its icy cold water with sea temperatures varying between 8-14 ^{0}C (Brown & Jarman 1978). Adjacent to this coastal strip an extensive coastal lowlands area stretches inland reaching the Cape Fold Mountains in the east (Figure 2). These lowlands are generally characterized by level plains lacking orographic features of high altitude, the exceptions being Kasteelberg and Piketberg Mountains with summits of almost 800m above sea level. The eastern part of the study-area is occupied by the Cape Fold Mountains, many parts of which are in the proximity of 1 000 m above sea level.

Mouton (1986b) reports that there is no indication that populations of melanistic taxa in the south-western Cape are background colour-matched. He maintains that there is no corresponence between the geographical distribution of melanistic populations and soil or parent rock colour, nor vegetation type. Although the possibility that causal factors other than climatic ones were involved in the evolution of melanism, seems remote (Mouton 1986b; Mouton & Oelofsen 1988), this has not been proved beyond doubt. The conclusions of Mouton (1986b) were based on indirect, macroscale observations and for a more realistic appraisal of the cryptic significance of melanism, attempts should be made at quantifying the colour of the lizards and their background.

It is today generally accepted that, being ectothermic, temperature plays an important role in the distribution of lizards (Poynton 1964, 1969; Stuckenberg 1969; Poynton & Bass 1970; Poynton & Broadley 1978). From Figure 3, showing the mean annual daily temperatures recorded at the 117 weather stations in the study-area, it is evident that sharp temperature gradients may exist even over short distances. It is therefore difficult to come to general conclusions regarding isotherms in the study-area. Nevertheless, it is clear that the immediate coastal regions, including the southern coastal lowlands, are generally cooler with mean daily temperatures varying from 15-17.5 ^{0}C. The western coastal lowlands, especially the more inland areas, on the other hand, are notably warmer with mean daily temperatures of 17.5-20 ^{0}C. Along the Cape Fold

Mountains mean temperatures are drastically influenced by altitude, being normally cooler at higher altitudes.

The distribution of melanistic cordylid populations in the study-area (Figure 1) is therefore, on a macroscale, obviously temperature correlated, these lizards being restricted to insular and peninsular situations and coastal rock (C. niger and C. polyzonus) and relatively high altitudes in the Cape Fold Mountains (Pseudocordylus capensis and C. oelofseni).

The occurrence of melanistic lizard populations in insular and peninsular situations is well documented worldwide. Mertens (1934) maintains that the surrounding water mass will have such a stabilizing effect on island temperatures that darker coloured lizards will have a positive selective value due to their greater capacity to utilize radiant heat. His view is supported by observations from Carlquist (1965) and Edelstam (1976). Unfortunately the paucity in temperature data, especially from the Saldanha-Langebaan areas, makes it difficult to check whether the Saldanha-Langebaan and Cape Peninsulas and the various islands along the coast in fact experience lower mean temperatures than adjacent mainland areas.

The climates of the western coastal regions are strongly influenced by the Cold Benguela Current. Associated with the Benguela Current, upwelling zones of even colder waters occur as semi-permanent features especially during summer months when S and SE winds are predominant (Andrews & Hutchings 1980). Three such major upwelling zones occur along the south-western Cape coastline (Taunton-Clark 1982) (Figure 4). Along the Cape Peninsula coast upwelling occurs from Duiker Point to Oudekraal where water temperatures of 9 ^{0}C are recorded during summer months. Another upwelling tongue occurs along the Saldanha-Langebaan coastal area, stretching from Yzerfontein in the south to about 20 km north of Cape Columbine, where water temperatures of 10 ^{0}C are recorded. Furthermore, a narrow zone of upwelling water occurs between Dwarskersbos in the south to immediately north of Elands Bay, with water temperatures of 11-12 ^{0}C.

It is immediately obvious that all the melanistic cordylid populations along the coast occur on islands in or on the mainland adjacent to these upwelling zones (Figure 4). There is thus a strong possibility that melanism is related to environmental conditions elicited by these upwelling zones. Although supportive temperature data are lacking, the Elands Bay, Saldanha-Langebaan and Cape Peninsula areas probably experience lower mean temperatures than adjacent areas as a direct result of the effect of the upwelling zones on the climate of these areas. A darker skin colour would be advantageous for any ectotherm under such circumstances.

The fact that the population of C. cordylus occurring on Robben Island is not melanistic (Mouton 1987), demonstrates that the island situation per se is not necessarily inducive to melanism as maintained by Mertens (1934). Robben Island lies outside the Cape Peninsula upwelling zone and as such experiences warmer surrounding water temperatures.

The paucity in temperature data makes the interpretation of the distribution of inland melanistic taxa difficult. From Figure 1 it is, however, clear that these populations invariably occur at higher altitudes along the Cape Fold Mountains and outliers thereof. Numerous studies have shown that altitude may have a decisive effect on mountain climates (Fuggle 1981). Cloudy, cold and wet conditions are generally characteristic of such areas (Barry 1981; Barry & Chorley 1982). According to Fuggle (1981) mean annual temperature decreases by 0.36 ^{0}C per 100 m increase in altitude. It is therefore justifiable to assume that all the inland melanistic cordylid populations, because of the relatively high altitudes at which they occur (at least 500 m above sea level) are subjected to lower mean temperatures than would have been the case at lower altitudes.

The distribution of non-melanistic taxa of the genera Cordylus and Pseudocordylus in the study-area suggests that melanism is not a prerequisite to survival in areas presently occupied by melanistic populations. Cordylus cordylus for example not only occurs on Robben Island and in the Saldanha-Langebaan area, but also at places at high altitudes in the Cape Fold Mountains (Mouton 1987; Mouton & Oelofsen 1988). In general, however, the non-melanistic taxa are most numerous along the warmer coastal lowlands

(C. cordylus and non-melanistic colour morphs of C. polyzonus) and lower mountain slopes (P. microlepidotus), areas where melanistic populations do not occur.

As all members of the genera Cordylus and Pseudocordylus are heliothermic, direct solar radiation is utilized to obtain preferred body temperatures during times of activity. Unfortunately only one weather station in the study-area records radiation, but mean annual sunshine hours per day were obtained from 56 stations. These data were used as an indication of available solar energy at these stations (Figure 5). In spite of the paucity in data for coastal and mountain areas, it is clear that the Saldanha-Langebaan and Cape Peninsula regions, inhabited by melanistic forms, receive less sunshine (6-8 hours per day) than adjacent areas on the coastal lowlands (8-9.5 hours per day). Areas along the extreme western flank of the Cape Fold Mountains and the Piketberg Mountains, where melanistic populations also occur, also receive lower mean annual sunshine hours (7-8 hours per day) than the coastal lowlands.

Data on cloud cover and fog have also been obtained from various stations in the study-area and would provide a clearer perspective of available solar radiation in different parts of the study-area. It is well-known that cloud cover can, if thick and complete enough, form a significant barrier to radiation, especially in the infrared part of the spectrum (Barry & Chorley 1982). According to Monteith (1973) a deep layer of stratus cloud can reflect as much as 70% of incident sunlight from its upper surface, about 20% may be absorbed within the cloud leaving only 10% for transmission to the surface. These results were manifested by aircraft measurements indicating that the proportion of incident radiation that is reflected, ranges from 44-55% for airostratus to 90% for cumulonimbus, while infrared radiation is extensively absorbed by water vapour and carbon dioxide (Barry & Chorley 1982).

In the south-western Cape heavy advective sea fog is a frequent phenomenon along the Benguela coast with a mean of 184 days per annum on Table Mountain, 128 days per annum at Saldanha Bay and 110 days per annum at Cape Columbine (Scheurkogel, Page, Schumann, Tebutt & Thomas 1973). The incidence of fog in the study-area is depicted in Figure 6 and it is noteworthy that a high incidence of fog is particularly prominent along the upwelling zones. Presumably this results from the rapid cooling of warm, moist airstreams when moving over the cold upwelled waters.

As all the coastal melanistic populations in the study-area occur in association with the upwelling zones, they are subjected to a high incidence of advective sea fog. Under conditions of steady light winds sea fog may persist for several days along these coastal regions (Barry & Chorley 1982).

The restraining effect of cloud and fog on solar radiation may seriously affect the heat budget of heliothermic lizards. According to Bogert (1949) regions with prevailing overcast and cloudy conditions are unsuitable habitats for reptiles with a high body temperature requirement. Moreover, Cole (1943) maintains that climatic conditions generally set rigid limits to the range of possible animal colours adopted by a species in that specific habitat. The association of darkly coloured lizards with humid, cloudy regions is well-documented (Mertens 1934; Parker 1935; Cole 1943; Edelstam 1976; Hoppe 1979). Parker (1935) considers shade to be the essential condition for dark colours to opperate advantageously. Melanism may thus be considered a great advantage for lizards occupying areas under the influence of the upwelling zones and associated high incidence of fog.

Because of the warmer temperatures of the adjacent interior and the general absence of land breezes, advective sea fog seldom reach inland areas far from the coast (Figure 6). Cloud caps of orographic fog or cloud may, however, be formed on high mountain slopes and summits further inland under prevailing SE, S, SW and NW winds with copious moisture (Heydorn & Tinley 1980). This process takes place when an air parcel is displaced to an environment of lower pressure, for example high mountain peaks, and its volume increases and temperature decreases. This process, known as adiabatic cooling, induces condensation with prolonged temperature reduction (Barry & Chorley 1982). Unfortunately, normal rain guages do not measure this type of moisture deposition. Consequently numerical data from weather stations in the study-area are very limited. Nagel (1956), using special traps of wire mesh or louvres to capture orographic fog, reported a fog drip of 5664 mm per annum on Table Mountain. Since this is three times more than the annual rainfall of this region (Schultze & McGee 1978), it can be concluded that orographic fog is a very important ecological agent in mountains. Therefore, it would not be unreasonable to expect orographic fog to be dynamic on high mountain ranges elsewhere in the study-area. Through personal observation (P.le F.N. M.) it has been established that the Hottentots Holland Mountains where the melanistic species C.niger and P.capensis occur, for example, are frequently covered in cloud during summer months, particularly when a strong south-easterly wind is blowing. Periods of cloud cover as long as two weeks have been noted. These observations are confirmed by the findings of Fuggle (1981) that high rainfall records are associated with mountain stations. The marked feature of rainfall under strong orographic control is well demonstrated by profile diagrams (Heydorn & Tinley 1980, p.9), where the rainfall curve follows the relief undulations closely.

Considering the fact that montane melanistic populations invariably occur at high altitudes in the study area, we can safely assume that they experience cloudy conditions associated with rain frequently. This would greatly affect the amount of solar radiation available to these lizards and a dark skin would be advantageous under such conditions.

Forced convection induced by wind is a major determinant of heat loss in lizards (Gates 1980) and one would expect that prevailing wind patterns will be a major determinant of lizard distribution. According to Fuggle (1981), however, no generilization can be made about winds in the south-western Cape, directions and speeds vary widely, both with season and location. Strong winds are characteristic of the entire coastal belt, with gale force S to SE winds dominating during summer and N to NW winds prevailing during most of the winter (Hydrographic Dept., London, 1954, 1963; Harris 1978; Heydorn & Tinley 1980; Fuggle 1981). With the data at our disposal we were accordingly unable to establish a correspondence between wind patterns and the geographical distribution of melanistic cordylid populations.

Cronjé and Mouton (under review) established that the two melanistic species, C. niger and C. oelofseni, had peaks of activity earlier in the morning than the non-melanistic species, C. cordylus, and during overcast weather became active at least two to three hours earlier than the latter. In light of the results obtained in our study, one therefore has to conclude that melanism infers upon its bearers certain qualities to prolong times of activity under the adverse conditions of lower temperatures and limited solar radiation.

Cronjé & Mouton (under review) furthermore point out that melanism is probably not a prerequisite for inhabitation of areas presently occupied by the melanistic forms, implying that melanism probably evolved under more adverse conditions than the present. They maintain that the present environmental conditions at the localities occupied by melanistic populations must be considered near the upper limits of the range acceptable for the species. The mere fact that all the melanistic taxa presently occur in the form of small isolated populations, suggest that these taxa are subjected to intense environmental pressures, bearing in mind that isolated melanistic populations of polymorphic cordylid species are not ecotypes but genealogically related.

The melanistic species, Cordylus niger, occurs in the form of two isolated populations in the Cape Peninsula and in the Saldanha-Langebaan area, respectively (Mouton 1987; Mouton & Van Wyk 1990) (Figure 1). Mouton & Oelofsen (1988) rules out the possibility of accidental transportation of individuals from one locality to the other and maintain that these two populations are remnants of a large melanistic population which must have frequented the south-western coast from the Cape Peninsula northwards to at least Saldanha Bay. Similarly, C. oelofseni, which today occurs in the form of small isolated populations along the extreme western flank of the Cape Fold Mountains, from Landdroskop in the south to the Piketberg Mountains in the north (Figure 1), must once have been one continuous population. Furthermore, Mouton & Oelofsen (1988) believe that the two melanistic species C. niger and C. oelofseni are sister species, because they share several non-adaptive character states. If this is indeed the case it would mean that melanism probably is an autapomorphy which developed in the ancestral species before vicariance and the speciation event which gave rise to the two extant species. This implies that a large melanistic ancestral population must at some stage have frequented the coastal lowlands from the coast to the Cape Fold Mountains prior to vicariance (Mouton & Oelofsen 1988).

All indications are therefore that similar climatic conditions presently experienced in association with the upwelling zones, must at some stage in the past have been characteristic of most of the study-area. Furthermore, these conditions probably prevailed all along the western coastal regions as far as the Orange River in the north.

Information on climatic changes during the Late Pleistocene and Holocene suggests that the extent of the polar ice sheets fluctuated in the form of regular pulses with a periodicity of some 100 000 years (Van Donk 1976; Imbrie & Palmer-Imbrie 1979). Glacial periods of cooler and drier climates were interrupted by shorter periods of warmer and generally wetter climates (Hays, Imbrie & Shackleton 1976; Kukla 1977). From approximately 40 000 BP cool moist conditions prevailed until the onset of the Last Glacial Maximum from about 25 000 - 17 000 BP (Deacon & Deacon 1986). The Last Glacial reached its peak at approximately 18 000 BP when conditions were the most severe of the glacial cycle and were essentially cold and dry, with temperatures 5-6 ^{0}C lower than at present (Deacon 1983a; Deacon & Deacon 1986; Tyson 1986). A relatively rapid amelioration of the climate took place after 16 000 BP (Deacon 1983b; Deacon & Deacon 1986), with a renewed onset of humidity which came to an end at about 11 000 BP (Vogel 1985). Finally, two wet/dry cycles followed with the highest temperatures in the mid-Holocene time at approximately 5 000 BP (Vogel 1985).

It is our contention that lower temperatures per se along the south-western coastal regions would not have been a primary factor in the evolution of melanism in cordylid lizards. Although information is available only for a few species, it is believed that most Cordylus and Pseudocordylus taxa display bimodal activity patterns, being active during the cooler early morning and late afternoon hours (Burrage 1974; Cronjé & Mouton under review). A mere shift in activity times towards an unimodal pattern would account for lower temperatures without a change in body coloration being necessary. We are of opinion that limited sunshine hours, especially during the summer months, was the primary force behind the evolution of melanism. This is in agreement with the view of Parker (1935) that shade is an essential condition for dark colours to operate advantageously.

Dating of the period when the south-western coastal regions were subjected to prolonged spells of intensive fog and cloud cover, which led to the evolution of melanism, would be difficult. As a rule, coloration in lizards is subjected to strong environmental pressures (Porter 1972; Endler 1978) and relatively quick changes in coloration may result from a change in climate. We therefore assume that the observed melanism did not evolve in the very distant past and that the conditions of limited sunshine hours probably prevailed during the Last Glacial Period or shortly after that.

When discussing the climates of the Last Glacial Maximum it must be borne in mind that the sea level was at least 130 m lower than at present (Tankard 1976). Both the extent of the coastal lowlands and the continental shelve would have been distincly different from the present and the influence of the Benguela Current and upwelling zones on the climate of the coastal regions would likewise have differed.

In summary, coastal melanistic populations in the study-area are associated with the upwelling zones in the Atlantic ocean. Direct effects of the upwelling zones on the climates of the adjacent coastal areas include lower mean daily temperatures and a high incidence of advective sea fog with resultant limitations on available solar energy. The montane melanistic populations, at the relatively high altitudes where they occur, also have to contend with lower mean daily temperatures and limited solar radiation owing to a high incidence of orographic fog and cloud cover. It is our contention that these conditions of limited sunshine hours and lower mean temperatures, some time in the past, were characteristic of the entire south-western coastal region.

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Figure 5. Mean annual sunshine hours recorded at 56 weather stations in the study-area.

Figure 6. The occurrence of advective sea fog recorded at 30 weather stations in the study-area.

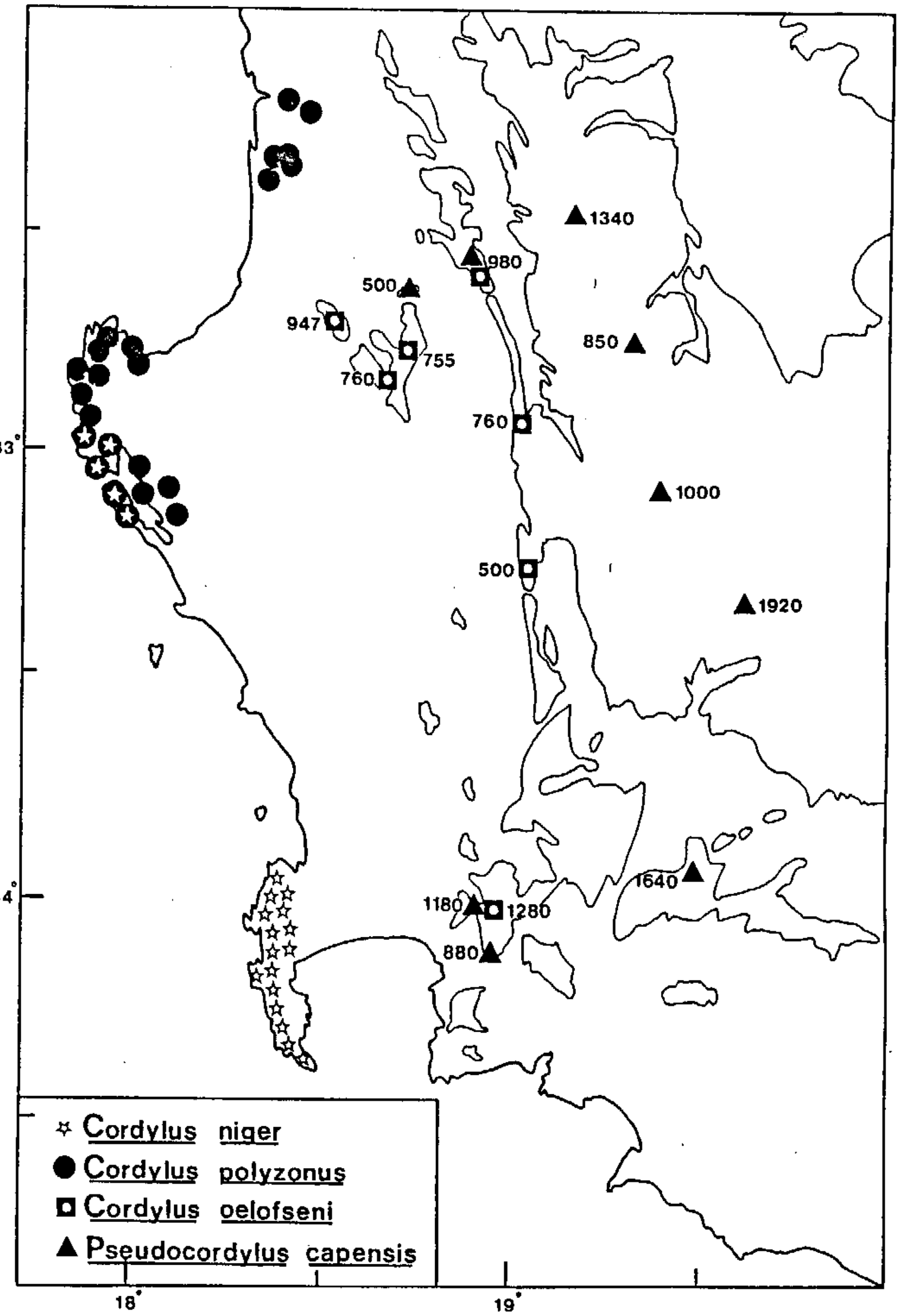
1340
980
500
947
755
850
760
760
33°
1000
500
1920
34°
1640
1180
1280
880
Cordylus niger
Cordylus polyzonus
Cordylus oelofseni
Pseudocordylus capensis
18°
19°

Figure 1.

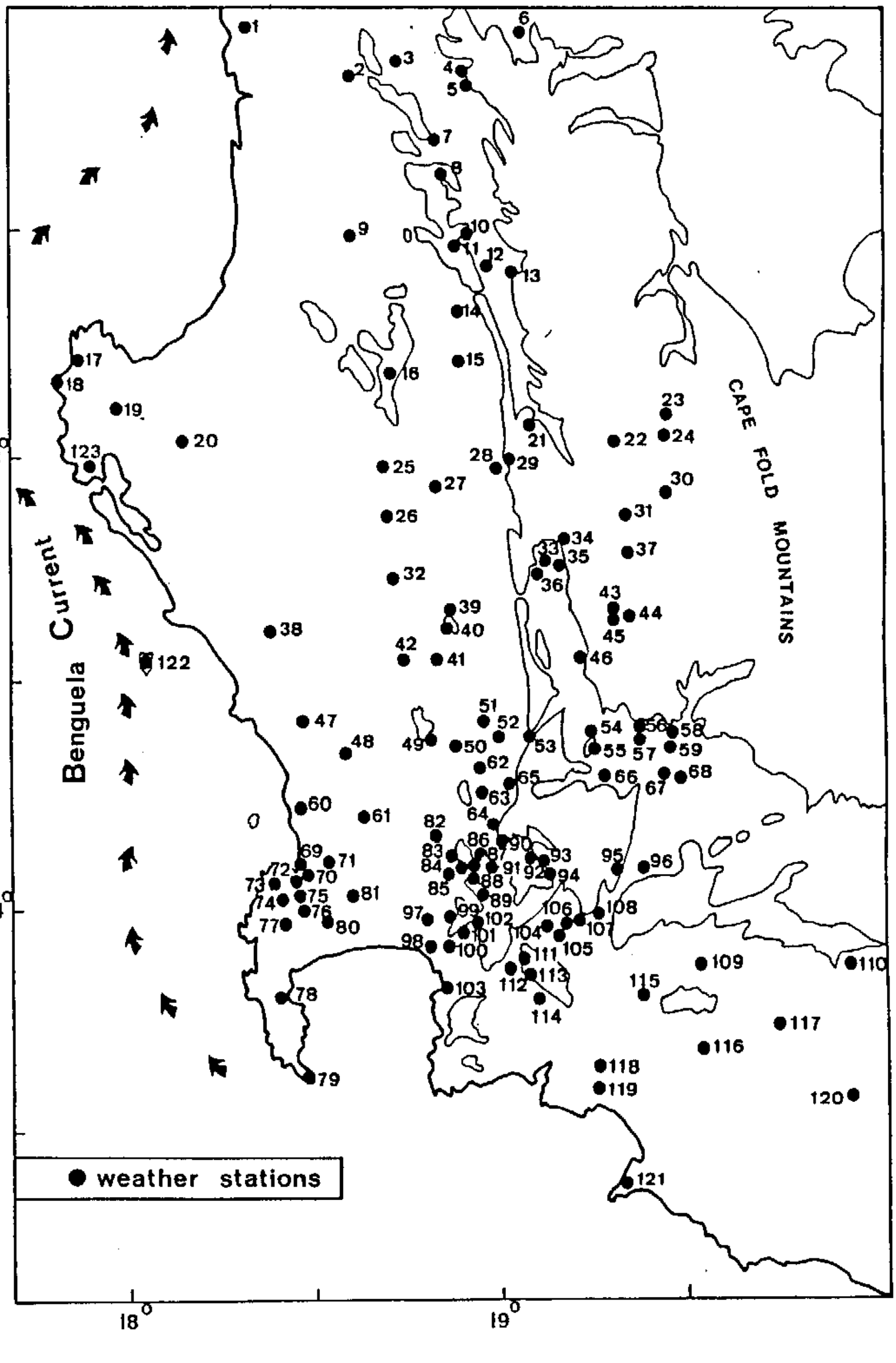
Benguela Current
CAPE FOLD MOUNTAINS
weather stations
33°
34°
18°
19°

Figure 2.

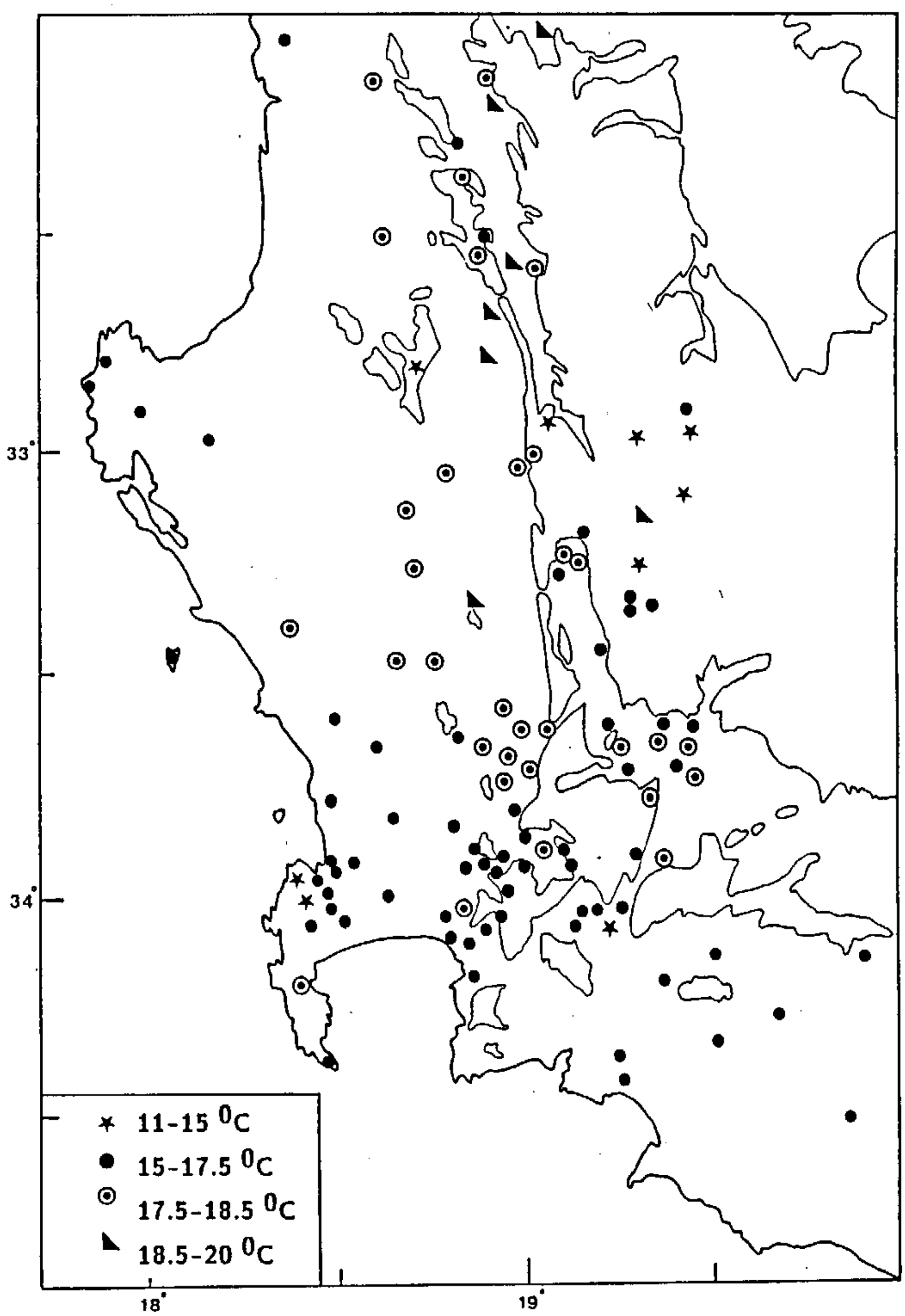

Figure 3

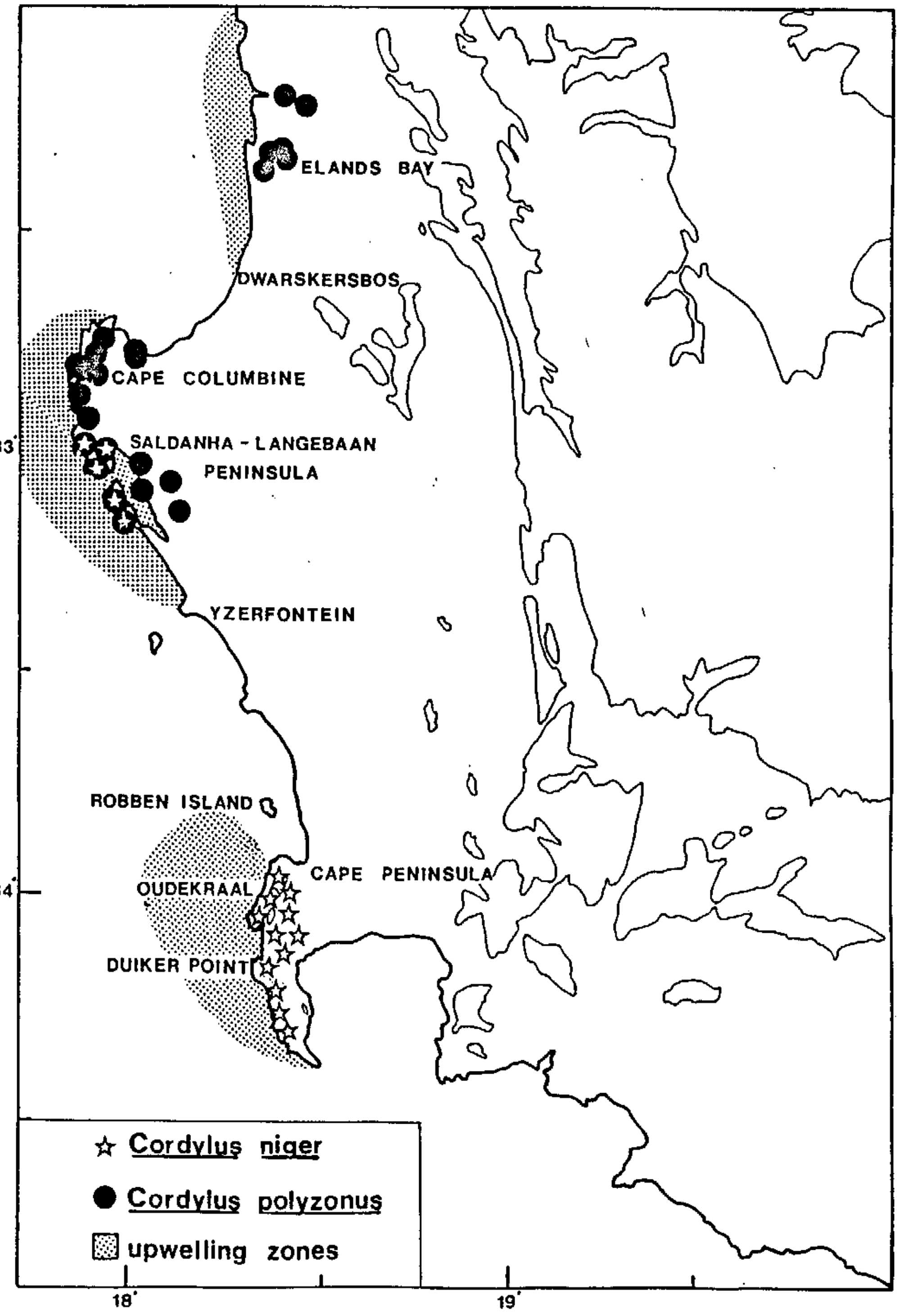
ELANDS BAY
DWARSKERSBOS
CAPE COLUMBINE
33°
SALDANHA - LANGEBAAN
PENINSULA
YZERFONTEIN
ROBBEN ISLAND
CAPE PENINSULA
34°
OUDEKRAAL
DUIKER POINT
☆ Cordylus niger
● Cordylus polyzonus
upwelling zones
18°
19°

Figure 4.

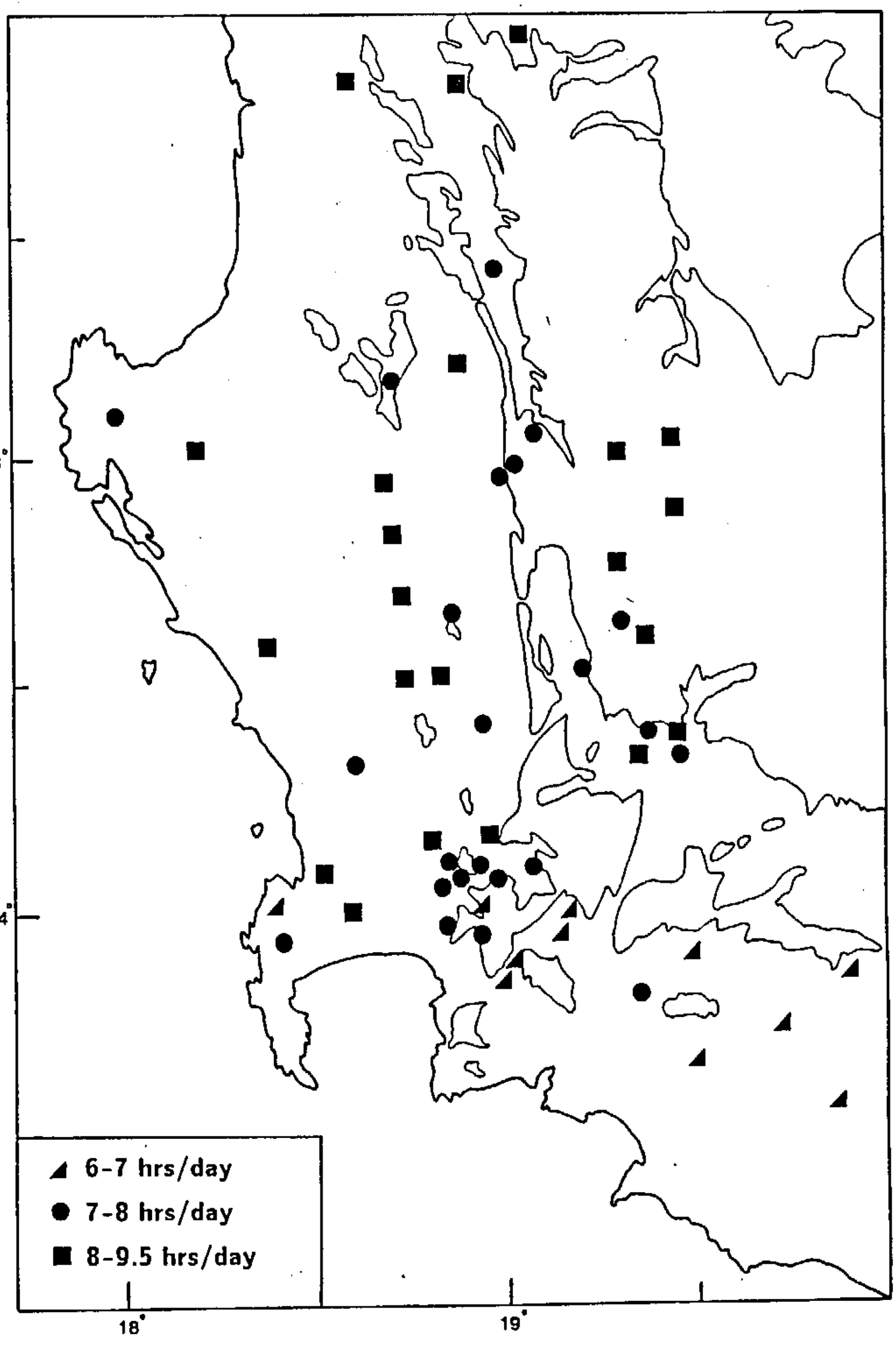

Figure 5.

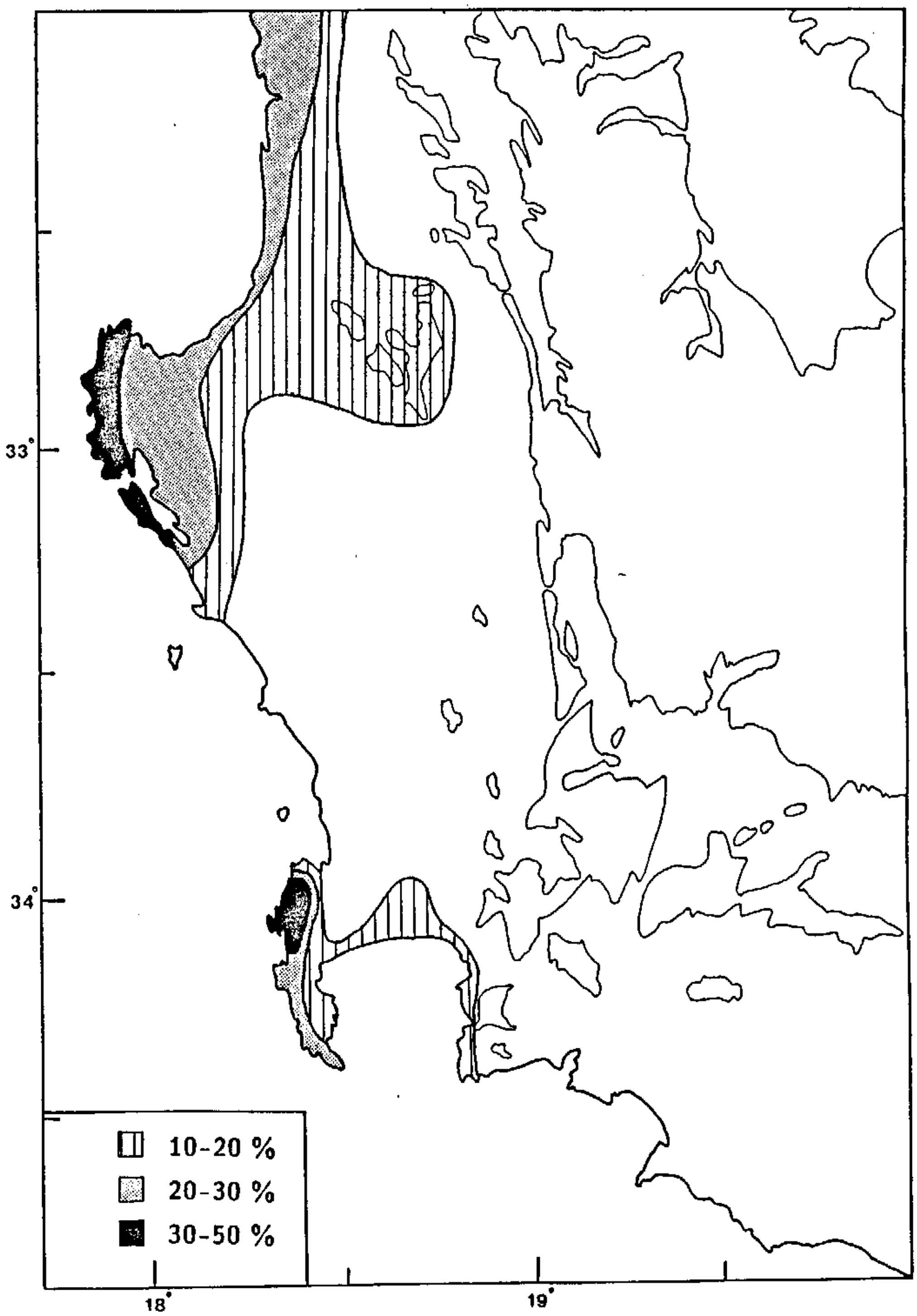

Figure 6.

APPENDIX 1: Weather stations in the study area.

1. Nortier : 3202S/1820E : 98m.
2. Graafwater Koop : 3210S/1836E : 177m.
3. Zeekoevlei : 3208S/1843E : 370m.
4. HLS Augsberg : 3210S/1854E : 92m.
5. Clanwilliam : 3211S/1854E : 75m.
6. Lorraine : 3203S/1903E : 320m.
7. Middeltuin : 3218S/1850E : 396m.
8. Tierkloof : 3222S/1851E : 610m.
9. Afgunst : 3230S/1836E : 31m.
10. Stagmanskop : 3230S/1854E : 587m.
11. Sewefontein : 3231S/1854E : 617m.
12. Citrusdal (NIVV) : 3234S/1859E : 198m.
13. Citrusdal Koop : 3235S/1901E : 170m.
14. Eendekuil : 3241S/1853E : 150m.
15. Ideal Hill : 3248S/1853E : 152m.
16. Heldervue : 3249S/1843E : 755m.
17. Paternoster : 3248S/1754E : 15m.
18. Cape Columbine : 3250S/1751E : 50m.
19. Vredenburg Koop : 3254S/1800E : 128m.
20. Langebaanweg : 3258S/1810E : 31m.
21. Heidedal : 3256S/1904E : 725m.
22. De Keur : 3258S/1918E : 945m.
23. Sneeuwkop : 3255S/1927E : 966m.
24. Excelsior : 3257S/1927E : 953m.
25. Koringberg : 3301S/1841E : 128m.
26. Moorreesburg Koop : 3309S/1841E : 158m.
27. Rooihoogte Noord : 3305S/1850E : 45m.
28. Porterville Mun. : 3301S/1900E : 137m.

29. Porterville Koop : 3301S/1901E : 145m.

30. Loch Lynne : 3305S/1927E : 975m.

31. De Hoek: 3309S/1902E : 115m.

32. Langgewens (WRS) : 3317S/1842E : 177m.

33. Waveren : 3315S/1907E : 178m.

34. Mont Rouce : 3312S/1910E : 320m.

35. Drostdy Wynkelder : 3315S/1909E : 190m.

36. Mont Pellier : 3316S/1906E : 151m.

37. Gydo : 3313S/1920E : 975m.

38. Darling : 3323S/1823E : 110m.

39. Riebeek-Wes Koop : 3321S/1852E : 168m.

40. Goedgedacht : 3323S/1851E : 370m.

41. Grasrug : 3328S/1850E : 213m.

42. Malmesbury : 3328S/1844E : 152m.

43. Riverside : 3321S/1918E : 457m.

44. Deelville : 3321S/1920E : 480m.

45. Ceres : 3322S/1918E : 456m.

46. La Plaisante : 3327S/1912E : 260m.

47. Atlantis : 3336S/1829E : 149m.

48. Philadelphia Pol : 3340S/1835E : 76m.

49. Slent : 3338S/1849E : 244m.

50. HLS Boland : 3339S/1852E : 149m.

51. Landau : 3336S/1858E : 122m.

52. Wellington : 3338S/1900E : 116m.

53. Welvanpas : 3338S/1904E : 221m.

54. Klipheuwel : 3338S/1914E : 265m.

55. Slanghoek Kelders : 3339S/1914E : 880m.

56. Driehoek : 3337S/1921E : 221m.

57. Shalvah : 3338S/1922E : 220m.

58. Worcester : 3338S/1927E : 236m.

59. Veldreserwe : 3339S/1927E : 275m.

60. Bloubergstrand : 3348S/1828E : 15m.

61. Diemersdal : 3348S/1838E : 152m.

62. Vredenhof : 3342S/1857E : 154m.

63. Bellevue (NIWW) : 3345S/1857E : 152m.

64. Bien Donne : 3350S/1859E : 138m.

65. Nederburg : 3343S/1901E : 183m.

66. Du Toitskloof Wynkelder : 3342S/1916E : 253m.

67. Brandvlei Dam : 3342S/1927E : 213m.

68. Aan-De-Doorns Wynkelder : 3342S/1929E : 220m.

69. Cape Town City Hospital : 3354S/1825E : 16m.

70. Cape Town S.A. Observatory : 3356S/1829E : 12m.

71. Wingfield : 3354S/1832E : 17m.

72. Table Mountain Devil's Peak : 3357S/1827E :431m.

73. Table Mountain Cable Way : 3357S/1824E : 1067m.

74. Table Mountain House : 3359S/1824E : 761m.

75. Kirstenbosch Bot : 3359S/1826E : 89m.

76. Wynberg : 3400S/1828E : 76m.

77. Groot Constantia : 3402S/1825E : 99m.

78. Simonstown Mun : 3412S/1826E : 30m.

79. Kaappunt : 3421S/1830E : 226m.

80. Kaapse Vlakte : 3402S/1832E : 30m.

81. D.F. Malan : 3359S/1836E :42m.

82. Elsenburg : 3351S/1850E : 177m.

83. Nietvoorbij (NIWW) : 3354S/1852E : 146m.

84. Helderfontein (NIVV) : 3355S/1853E : 179m.

85. Welgevallen II : 3356S/1851E : 116m.

86. Mountain Vineyards : 3353S/1857E : 362m.

87. Glen Arum : 3355S/1855E : 396m.

88. Dellaire : 3356S/1855E : 450m.

89. Jonkershoek : 3358S/1856E : 244m.

90. Groot Drakenstein : 3352S/1900E : 146m.

91. Bethlehem : 3355S/1858E : 376m.

92. La Motte : 3353S/1905E : 206m.

93. Franschoek : 3354S/1906E : 244m.

94. Keerweder : 3356S/1907E : 335m.

95. High Noon : 3355S/1918E : 580m.

96. Fismershof : 3355S/1922E : 314m.

97. Helderberg : 3402S/1848E : 76m.

98. Somerset-West : 3405S/1849E : 8m.

99. Nooitgedacht : 3402S/1851E: 343m.

100. Bizweni : 3405S/1851E : 46m.

101. Lourensford : 3404S/1853E : 107m.

102. Vergelegen : 3403S/1855E : 85m.

103. Steenbras Dam : 3411S/1851E : 339m.

104. Riviera : 3403S/1908E : 315m.

105. Chiltern Damwal : 3403S/1909E : 309m.

106. Longdown : 3403S/1910E : 341m.

107. Klipfontein : 3402S/1911E : 343m.

108. S.O.S. : 3401S/1913E : 317m.

109. Serjeantsrivier : 3408S/1931E : 366m.

110. Tygerhoek (WRS) : 3408S/1954E : 168m.

111. Elgin (NIVV) : 3408S/1902E : 305m.

112. Elgin Bos : 3409S/1901E : 281m.

113. Applegarth : 3409S/1903 : 310m.

114. Kromvlei : 3412S/1905E : 270m.

115. Boontjieskraal : 3412S/1921E : 128m.

116. Dunghye Park : 3419S/1931E : 122m.

117. Hooggelee : 3416S/1942E : 351m.

118. Oude Hemel & Aarde : 3421S/1914E : 243m.

119. Braemer : 3423S/1914E : 84m.

120. Jonaskraal : 3424S/1954E : 103m.

121. Danger Point : 3437S/1918E : 28m.

122. Dassen Island : 3326S/1805E : 5m.

123. Saldanha : 3300S/1800E : 60m.

ONTOGENETIC AND SEASONAL COLOUR CHANGE IN THE GIRDLED LIZARD, *CORDYLUS POLYZONUS*, FROM THE SOUTH-WESTERN CAPE, SOUTH AFRICA

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Differences in reflectivity of the dorsal skin between melanistic and turquoise forms of the species, Cordylus polyzonus, have been quantified and ontogenetic colour change in the melanistic form is discussed. Experiments to investigate short term colour change, with temperature as variable, produced no conclusive results. Seasonal changes in dorsal skin reflectivity was, however, demonstrated for both the melanistic and turquoise forms, indicating that this species has the physiological capacity to change colour. It is suggested that geographic variation in colour in this species cannot be attributed to this capacity but probably is the result of selection over time.

Verskille in reflektiwiteit van die dorsale vel tussen melanistiese en turkoois vorme van die spesies, Cordylus polyzonus, is gekwantifiseer en ontogenetiese kleurverandering in die melanistiese vorm word bespreek. Uit die resultate van eksperimente waarin korttermyn kleurverandering ondersoek is, met temperatuur as veranderlike, kon geen finale afleidings gemaak word nie. Daarenteen is seisoenale veranderinge in dorsale vel reflektiwiteit in beide melanistiese en turkoois vorme suksesvol demonstreer, wat beskou kan word as 'n aanduiding van die fisiologiese kapasiteit van hierdie spesies om van kleur te verander. Daar word gereken dat geografiese variasie in kleur wat in hierdie spesies voorkom nie aan hierdie kleurveranderings-kapasiteit toegeskryf kan word nie, maar waarskynlik die gevolg is van seleksie oor tyd.

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INTRODUCTION

Two main hypotheses have been advanced to explain colours of lizards. Colour may provide protection from predators through background colour-matching, countershading, warning colours, pattern matching and mimicry (Porter 1972; Hoppe 1979). On the other hand coloration also plays an important role in the thermoregulation of all ectotherms through the differential reflection and absorption of incident radiation (Norris 1967; Porter 1972; Hoppe 1979). Bartlett & Gates (1967), for example, reported that the total energy gain of a lizard would be altered by about 4% with a 10% change in the lizard's absorptivity.

Most studies on the role of colour in reptile thermoregulation have been done to determine the significance of metachrosis (ability to change colour). Pioneering work in this regard was done by Atsatt (1939) who studied 16 species of lizards displaying metachrosis and who discovered that they respond to high temperatures by assuming their light phase and to low temperatures by assuming their dark phase. In most of these earlier studies (Parker & Starratt 1904; Parker 1938; Wilson 1940) coloration was appraised either by visual perception or by using colour atlases. Since animal skin colour results from both coloured pigments and fractionation of light, together with additional dimensions added by the eye and brain of the observer, these methods are considered either imprecise or subjective (Norris 1967). Norris (1958) was one of the first investigators to quantify skin colour of living reptiles by measuring skin reflectivity in the visible spectrum (400-700 mμ) with a spectrophotometer. Results of this study revealed that there is a close correspondence between dorsal skin colour and background colour in fringed-toed sand lizards. Similar studies to quantify background colour-matching in reptiles and amphibians have been done by Talbot & Livezey (1963) and Norris & Lowe (1964).

Studies to measure reflectance beyond the visible spectrum (400-700 mμ), from near-ultraviolet through about 1500 mμ to near-infrared, were conducted by Bodenheimer (1952) and Bodenheimer, Halperin & Swirski (1953). Hutchison & Larimer (1960) recorded reflectivity of excised lizard skin over the spectral range from 300-1200 mμ, while Tercafs (1963) analysed transmission of shed reptile skins to ultraviolet, visible and infrared radiation. These studies led to the conclusion that colour changes associated with background colour-matching are mainly restricted to the visible part of the solar spectrum (400-700 mu) and changes in the infrared part of the spectrum (from 700 mμ upwards) with thermoregulation (Norris 1967).

Most studies on aspects of metachrosis concerned the lizard families Gekkonidae, Iguanidae, Agamidae and Chamaeleonidae where this phenomenon is well-developed in most species. No information on metachrosis is, however, available for the Cordylidae, a lizard family endemic to Africa. Recently, Mouton (1986) and Mouton and Oelofsen (1988) advanced hypotheses to account for melanism in the genera Cordylus and Pseudocordylus in the south-western Cape. They maintain that melanistic populations of these genera in this region, represent cold-adapted relicts from the Last Glacial Maximum (18-16 000 BP). These authors, however, did not verify whether real differences in reflectance in the near-infrared part of the spectrum exist between melanistic and non-melanistic taxa. Furthermore, they had no knowledge of the physiological capacity of these lizards to change colour over the short and long term. We are of opinion that such information is important for a clear perspective of the functional importance of melanism in cordylid species in the south-western Cape. The aim of our study accordingly was to investigate these aspects.

Cordylus polyzonus is a most variable species in terms of coloration and comprises both melanistic and non-melanistic forms. In the south-western Cape alone no less than four colour variants occur (Mouton 1986; Mouton & Oelofsen 1988) (Figure 1). In the Lamberts Bay-Elands Bay and Saldanha-Langebaan regions melanistic populations prevail, while immediately to the south and east, turquoise and brownish variations are to be found. In the Worcester-Villiersdorp area individuals of this species are reddish in colour. Badenhorst, Mouton & Van Wyk (under review a) pointed out the close correspondence between the occurrence of melanistic populations and the upwelling zones in the Atlantic ocean and maintain that the black body colour is advantageous in terms of thermoregulation in the conditions of lower temperatures and limited sunshine hours associated with these zones. The turquoise variation, on the other hand, is considered a warm-adapted form, frequenting the warmer inland regions.

The melanistic and turquoise variations of Cordylus polyzonus provide the opportunity to quantify differences in reflectance in the infrared part of the spectrum between melanistic and non-melanistic individuals. Furthermore, through personal observation (N.C.B.), confirmed by discussions with other workers, it has been noted that in this species there might be a slight change in body colour shortly after capture, while seasonal changes in body colour have also been noted. Moreover, juveniles of all four colour variants in the south-western Cape seem to be of similar coloration, with adult coloration developing only at a later stage. Cordylus polyzonus is accordingly considered a suitable experimental animal for the purposes of this study. Specimens of the melanistic and turquoise variations of this species were used to quantify differences in reflectivity in the infrared part of the spectrum. The same two colour variants were also used to investigate the ability to change colour over the short term as well as over the long term.

MATERIALS AND METHODS

All the experimental animals used in this study were collected from two localities in the south-western Cape, melanistic specimens from Jacobs Bay (32^{0}57'52"S;17^{0}52'50"E) and turquoise individuals from Klipberg (33^{0}20'00"S;
18^{0}17'56"E) (Figure 1).

Spectral reflectance of the dorsal skin surfaces of the animals was determined over the wavelenth interval 500-2500 mμ, using a Beckman DK-2A spectroreflectometer equipped with a tungsten lamp heat source and a lead sulfide detector cell. Before analyzing the samples, zero and 100% reflectivity were set with magnesium oxide blanks at the exit ports. Sample measurements were expressed as percentage reflectance in relation to the magnesium oxide blank.

To obtain the desired body temperature during recordings, the animals were secured onto a metal radiator tank (210 x 75 x 28 mm), using velcro strips. The temperature of the water circulating through the radiator was regulated by means of a HAAKE Heating Bath & Circulator (Model F3). Using this method body temperatures, which were measured by inserting a temperature probe connected to a Bailey Bat (Model BAT-12) into the cloaca, deviated from the selected values by no more than 0.5 ^{0}C during the scanning period. A special stainless steel plate with a 20 mm diameter opening, which fits tightly to the reference port of the spectroreflectometer, was secured to the back of each animal to be monitored. For juveniles a stainless steel plate of the same size was used, but the diameter of the opening was only 14 mm. The purpose of the stainless steel plate was to minimize interference of external light with the actual reading. Furthermore, by tracing the outline of the plate onto the back of the animal with permanent ink, reflectance of the same skin area could be measured in those experiments where reflectance was measured more than once for the same animal.

Seasonal colour change: During February, May, August and November 1989 a total of 49 melanistic and 36 turquoise C. polyzonus specimens were collected and spectral reflectance of the dorsal skin, over the range 500-2500 mμ, was determined for each individual shortly after capture. During the scanning period, the experimental animals were kept at room temperature. Mean reflectivity values of melanistic and turquoise specimens were compared at 100 mμ intervals to determine dorsal skin reflectivity differences between the two colour variants. The same set of spectral reflectances, treated separately for each month, was used to determine whether any seasonal reflectivity changes occurred within each colour variant.

Ontogenetic colour change: During March 1989, 11 melanistic and 5 turquoise juveniles were born in captivity. Spectral reflectance of the dorsal skin, over the range 500-2500 mu, was established for each individual whilst kept at room temperature. By comparing mean reflectivity differences between melanistic and turquoise juveniles with mean reflectivity differences between adults of the two colour variants, ontogenetic changes in reflectivity could be determined.

Short term colour change:

Experiment I: In order to investigate the effect of rapid temperature change on dorsal skin reflectivity, 10 specimens of each colour variant, captured during November 1988, were analyzed. After inserting a temperature probe in the cloaca of an individual and securing it with insolation tape to the tail, the specimen was cooled in a refrigerator to a body temperature of 5 ^{0}C. At reaching this temperature, the animal was secured onto the radiator tank, kept at the same temperature by cooled water circulating from the water bath. The reflectivity of the dorsal skin was measured over the spectral range 500-2500 mμ. Remaining in the same position, the animal's body temperature was raised to 30 ^{0}C by heating the water circulating through the radiator, and again the spectral reflectance was recorded. The heating process took approximately 40 minutes. Changes in dorsal skin reflectivity were determined by comparing the reflectance curves measured at 5 and 30 ^{0}C, of each individual, respectively.

Experiment II: The effect of longer term exposure to different environmental temperatures on changes in dorsal skin reflectivity was investigated in 15 melanistic and 12 turquoise specimens of C. polyzonus, collected during May 1989. Shortly after capture, half of the individuals of each colour variant were put in a temperature room at 16 ^{0}C, while the other half were subjected to 25 ^{0}C in another temperature room for a period of two weeks. Animals of the two colour variants were housed together in four identical glass vivaria (900 x 380 x 320 mm) with a photoperiod of 9L15D (8a.m. - 5p.m.) and with food and water available ad libitum. In each vivarium, natural light was simulated by using 15W growlights, emitting most of the spectral components of sunlight, while 100W infrared spotlights served as a heat source. Automatic timers switched the growlights on from 8a.m. - 5p.m., while the infrared spotlights provided heat from 9a.m. - 4p.m. every day. At the end of the two week period, dorsal skin reflectivity of each animal was determined over the 500-2500 mμ spectral range. Then the experimental groups were interchanged so that the specimens kept at 16 ^{0}C, now experienced an ambient temperature of 25 ^{0}C, and conversely. After completion of another two weeks, the reflectivity curve of each individual was recorded between 500-2500 mμ. Dorsal skin reflectivity changes in response to long term exposure to specific temperatures, were established by comparing reflectivity curves, recorded after two week's exposure to 16 and 25 ^{0}C, for each individual, respectively.

To ensure constant and accurate measurement by the spectroreflectometer throughout the study, regular wavelength calibration checks were performed using the same reference standard each time. Where applicable, Student's T-test was used to determine the statistical significance of differences between samples. P-values larger than 0.05 was taken as indicating non-significant differences and P-values smaller than 0.05 as indicating significant differences.

RESULTS

Differences in reflectivity of the dorsal skin between the melanistic and turquoise forms, in the spectral range 500-2500 mμ, are depicted in Figure 2. Both curves follow similar trends over the entire range with maximum reflectance between 1100-1200 mμ. Over the spectral range 500-1300 mμ highly significant differences in reflectance were recorded at each 100 mμ interval ($P < 0.05$), reflectivity in the melanistic form being markedly lower than in the turquoise form. This part of the spectrum comprises both visible and near-infrared wavelengths. In the longwave infrared zone, however, from 1400 mμ upwards, no significant differences between the two forms were found ($P > 0.05$ at each 100mμ interval).

Ontogenetic colour change: Reflectivity curves of melanistic and turquoise juveniles over the spectral range 500-2500 mμ are presented in Figure 3. In the range 500-1200 mμ no significant differences were recorded, but from 1200-1900 mμ, in the near-infrared to infrared regions, melanistic juveniles displayed significantly lower reflectivities than turquoise juveniles ($P < 0.05$). Although significant differences in reflectivity were also recorded at 2500 mμ, this is near the upper limit of the recording potential of the apparatus and were accordingly considered unreliable.

Short term colour change:

Experiment I: Differences in reflectivity of the dorsal skin at 5 ^{0}C and 30 ^{0}C are depicted in Figures 4a & 4b for melanistic and turquoise individuals, respectively. In both forms, no significant difference in reflectivity could be established at any point over the entire spectrum between these two temperatures. Average reflectances over the spectral range 700-1300 mμ, computed for each of the 20 experimental animals used in the analysis (Table 1), indicate that seven out of 10 melanistic and six out of 10 turquoise individuals displayed higher reflectivities at 30 ^{0}C than at 5 ^{0}C. These changes in reflectivity are, however, small (an average of 0.81% for the melanistic and 0.22% for the turquoise form).

Experiment II: Reflectivity curves for melanistic and turquoise individuals after two week periods of exposure to ambient temperatures of 16 ^{0}C and 25 ^{0}C, respectively, are depicted in Figures 5a & 5b. In both the melanistic and turquoise forms no significant change in reflectivity could be demonstrated. The average relectivities of each of the 15 melanistic and 12 turquoise individuals in the near-infrared zone (700-1300 mµ) are listed in Table 2. Slightly higher reflectivities were noted in 11 out of 15 melanistic and 11 out of 12 turquoise specimens after subjected to an ambient temperature of 25 ^{0}C in comparison with reflectivities recorded after the animals were subjected to an ambient temperature of 16 ^{0}C. These changes are, however, non-significant ($P > 0.5$). Over the range 700-1300 mµ, there still remained a highly significant difference in reflectivity between melanistic and turquoise forms at both temperatures ($P < 0.05$).

Seasonal colour change: Dorsal skin reflectivities of melanistic individuals over the spectral range 500-2500 mµ, recorded during the months February, May, August and November are presented in Figures 6a & 6b. Meaningful differences were observed only in the range 500-1300 mµ. During February the average reflectivity over this range of the spectrum was 17.63%, during May 16.48%, during August 15.50% and during November 17.09%. These values represent significant differences between all the months, except February and November ($P < 0.05$).

Reflectivities recorded for turquoise individuals (Figure 8b), in general followed the same trend as observed for melanistic individuals. Average reflectivity values determined for the spectral range 700-1300 mu are 23.11%, 22.28%, 19.31% and 20.81% for the months February, May, August and November, respectively. Only between the months February and May, do the average values differ significantly ($P < 0.05$).

DISCUSSION

According to Hutchison and Larimer (1960) 38-45.2% of solar energy is contained in the visible part of the spectrum (400-700 mµ), while the near-infrared part (700-1100 mµ) contains an additional 33.3-42.2%. The spectral range 400-1100 mµ accordingly accounts for up to 80% of the total energy received from solar radiation. From the results obtained in this study it is clear that melanistic individuals will be able to utilize this energy source to greater effect than turquoise individuals, the dorsal skin of melanistic individuals showing lower reflectivity than the latter over the spectral range 500-1300 mμ.

There is a wealth of literature on the thermoregulatory advantages of a dark skin. Cogger (1974), for example, reports that the expanded state of the melanophores of the mallee dragon (Amphibolurus fordi), yielding a darker colour, increases its efficiency of heliothermic basking. Gibson & Falls (1979) established that melanistic forms of the common garter snake, Thamnophis sirtalis, have an improved ability to convert solar radiation to body heat in comparison to striped individuals. These results are supported by several other investigations, showing that darker colours (lower reflectivity) have enhanced energy-absorbing properties in comparison to lighter colours (higher reflectivity) (Norris 1967; Porter 1967; Pearson 1977; Hoppe 1977).

As Cordylus polyzonus is a typical heliothermic lizard utilizing direct solar radiation as primary energy-source for thermoregulation, greater absorptive qualities of the dorsal skin surface will accordingly be a definite advantage in areas where conditions of lower mean temperatures or limited sunshine prevail. Our results therefore confirm the views of Mouton and Oelofsen (1988) that melanistic populations in the south-western Cape represent relict "cold-adapted" forms. It also ties in well with the observations of Badenhorst et al. (under review a) who demonstrated a close correspondence between the geographical occurrence of melanistic populations and upwelling zones in the Atlantic ocean with associated conditions of limited sunshine hours and lower mean daily temperatures.

Thermal physiology is considered to evolve slowly in reptiles and congeneric species from differing climates normally have similar preferred body temperature ranges (Bogert 1949; Spellerberg 1972; Heatwole 1976; Huey & Slatkin 1976; Schall 1977; Fuentes & Jaksic 1979). A change in body colour would be one way of surviving under sub-optimal conditions, without a change in preferred body temperature ranges being necessary.

Over the wavelength range 500-1200 mμ, which represents the visible to near-infrared parts of the spectrum, no significant differences in reflectivity between juveniles of the melanistic and turquoise forms were recorded, while a highly significant difference was demonstrated for adults of these two forms over the same range. Juveniles of the melanistic form are not black, but light green checkered with dark brown, therefore more or less similar in coloration to juveniles and adults of the turquoise form. This implies that in the melanistic form the black coloration develops later in life.

Furthermore, in the near-infrared to infrared range of the spectrum (1200-1900 mµ) significant differences in reflectivity were recorded between juveniles of the two forms, whilst in adults no such differences were found. Owing to different size openings used during recording, reflectivity values obtained for juveniles cannot be directly compared to that obtained for adult specimens. We were therefore unable to establish whether the change in reflectivity from juvenile to adult values involved the melanistic or turquoise variation, or both.

Few studies have been performed on the thermoregulatory significance of ontogenetic colour change in lizards. Fitch (1955) reported that hatchlings of the skink Eumeces obsoletes are usually jet black dorsally, while the adults have a much lighter coloration, and concluded that the darker coloration of juveniles, combined with their greater ratio of surface area to volume, allows more capacity for gaining heat through thermoregulatory behaviour, and results in an increased growth rate. Our results differ in an important aspect from that of Fitch, namely in that hatchlings are lighter in colour and that darker coloration develops only later in life. To explain this controversy it is important to have some idea of differential pressures exerted by the environment on lizard coloration. Mouton (1986) maintains that adult melanistic individuals of C. polyzonus are not backgroung colour-matched, in contrast to non-melanistic individuals which seem to blend in well with their environment. This suggests that the thermoregulatory function of colour overrides the protective function in adult melanistic individuals. The lighter coloration of hatchlings of the melanistic form may be interpreted as suggesting that the protective function of colour is more important in juveniles than the thermoregulatory one. The inverse relationship between body size and the rate of change in body temperature suggests that physiological control of body temperature would functionally be less important in small lizards than in large ones (Bartholomew 1982). The large surface to volume ratios of very small lizards causes their body temperatures to change so rapidly that physiological modification of rate of change is only of negligible importance in comparison with behavioural adjustments.

With the limited information available at this stage it would, however, be premature to come to any conclusions regarding the functional significance of ontogenetic colour change in the melanistic form of C. polyzonus. Our results have, however, indicated that it is a real phenomenon in this species. This is in contrast to other melanistic species such as C. niger, C. oelofseni, C. peersi and Pseudocordylus capensis where there is no ontogenetic colour change, the hatchlings being melanistic at birth.

Although it has been demonstrated that in those species displaying metachrosis, ambient temperature is a determining factor of colour change (see Norris (1967) and Hoppe (1979) for an overview) the intensity of direct solar radiation might be the most important factor. In our experiments to determine the physiological capacity of C. polyzonus individuals to change body colour in response to short term changes in the physical environment, the experimental animals were subjected to different ambient temperatures but similar radiation from infrared heat sources. The possibility, therefore, exists that in our experimental design those conditions inducive to colour change, have not been altered sufficiently to evoke a response. In fact, the observation that seasonal changes in reflectivity in both melanistic and turquoise forms do occur, indicate that this species has indeed some physiological capacity to change colour. In both forms reflectivity decreased during the cooler months of May and August, and increased during the warmer months November and February. This shows that the winter conditions of lower mean temperatures and lower availability and intensity of solar radiation can induce some colour change in this species.

Cronjé & Mouton (under review) maintain that heliothermic Cordylus species can probably cope with conditions of lower mean temperatures by a mere shift from a bimodal activity pattern to a unimodal pattern provided there is no limitation on the availability of direct solar radiation. Furthermore, Badenhorst et al. (under review a) demonstrated the close association of melanistic cordylid populations with a high incidence of fog or cloudcover. It follows that in future investigations special attention should be given to limited solar radiation as a determining factor of physiological colour change in C. polyzonus.

In summary, the difference in dorsal skin reflectivity over the spectral range 500-1300 mμ between the melanistic and turquoise forms of Cordylus polyzonus endorses the views of Mouton & Oelofsen (1988) that melanism in this species is an adaptation to adverse climatic conditions. Ontogenetic colour change in this species is unique for the genus as it has not been demonstrated for any other species. Although much more research in this field is needed, there is some indication in this species of a physiological capacity to change colour under changing climatic conditions. We are, however, of opinion that this ability cannot account for the distinct differences in reflectivity between the melanistic and turquoise forms, although these populations are subjected to differential environmental conditions. The observed differences in coloration must be the result of selection over time. This view is underscored by the studies of Badenhorst et al. (under review b) who demonstrated that, except for colour and body size, the melanistic and turquoise forms also differ in certain non-adaptive characters, suggesting that they do not belong to the same primary gene pool.

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Table 1: List of average dorsal skin reflectivities, in the near-infrared zone, of melanistic and turquoise *C. polyzonus* individuals at 5° C and 30° C.

MELANISTIC INDIVIDUALS

Individual	30° C	5° C	Difference
1	16.34	15.98	0.36
2	15.58	17.24	-1.66
3	16.70	16.97	-0.27
4	15.74	14.11	1.63
5	15.60	14.27	1.33
6	17.04	14.44	2.60
7	14.70	12.30	2.40
8	14.57	13.22	1.35
9	13.17	13.16	-0.01
10	16.04	15.66	0.38
AVG	15.54	14.73	0.81
STD	1.14	1.67	

TURQUOISE INDIVIDUALS

Individual	30 C	5° C	Difference
1	22.84	21.17	1.67
2	21.22	21.92	-0.69
3	20.07	20.14	-0.06
4	21.95	21.68	0.28
5	20.21	19.20	1.01
6	19.60	18.65	0.95
7	20.85	20.58	0.28
8	20.90	23.65	-2.75
9	21.15	21.30	-0.42
10	23.27	21.20	1.97
AVG	21.20	20.98	0.22
STD	1.18	1.43	

Table 2: List of average dorsal skin reflectivities, in the near-infrared zone, of melanistic and turquoise C. polyzonus individuals after two week's exposure to 16° C and 25° C ambient temperature.

MELANISTIC INDIVIDUALS

Individual	25° C	16° C	Difference
1	18.86	16.97	1.89
2	16.75	14.77	1.98
3	15.78	15.37	0.41
4	17.24	17.02	0.22
5	20.68	19.60	1.08
6	17.39	17.17	0.22
7	19.01	18.05	0.96
8	18.14	18.04	0.10
9	17.83	18.50	-0.67
10	17.80	18.42	-0.62
11	17.53	17.94	-0.41
12	17.47	15.31	2.16
13	18.94	18.64	0.30
14	19.43	18.18	1.25
15	17.71	18.12	-0.41
AVG	18.03	17.47	0.56
STD	1.19	1.38	

TURQUOISE INDIVIDUALS

Individual	25° C	16° C	Difference
1	23.57	23.14	0.43
2	22.26	22.01	0.25
3	22.63	22.22	0.41
4	23.71	23.24	0.47
5	25.38	23.85	1.53
6	22.34	21.74	0.87
7	20.94	20.92	0.02
8	20.92	21.77	-0.85
9	21.50	20.38	1.12
10	25.97	25.15	0.82
11	23.00	22.38	0.62
12	21.44	21.27	0.17
AVG	22.81	22.34	0.47
STD	1.63	1.33	

LIST OF FIGURES

Figure 1. Geographical distribution of the four colour variants of Cordylus polyzonus in the south-western Cape. Localities where melanistic and turquoise variants of Cordylus polyzonus were collected for this study, are indicated with an arrow.

Figure 2. Reflectivity curves of dorsal skin for adult melanistic and turquoise C. polyzonus specimens recorded at room temperature.

Figure 3. Reflectivity curves of dorsal skin for juvenile melanistic and turquoise C. polyzonus specimens recorded at room temperature.

Figure 4. Differences between dorsal skin reflectivity of a: melanistic and b: turquoise C. polyzonus specimens recorded at 5 ^{0}C and 30 ^{0}C.

Figure 5. Differences in dorsal skin reflectivity after two week's exposure periods to 16 ^{0}C and 25 ^{0}C ambient temperature for a: melanistic and b: turquoise individuals of C. polyzonus.

Figure 6. Seasonal reflectivity changes in a: melanistic and b: turquoise C. polyzonus individuals.

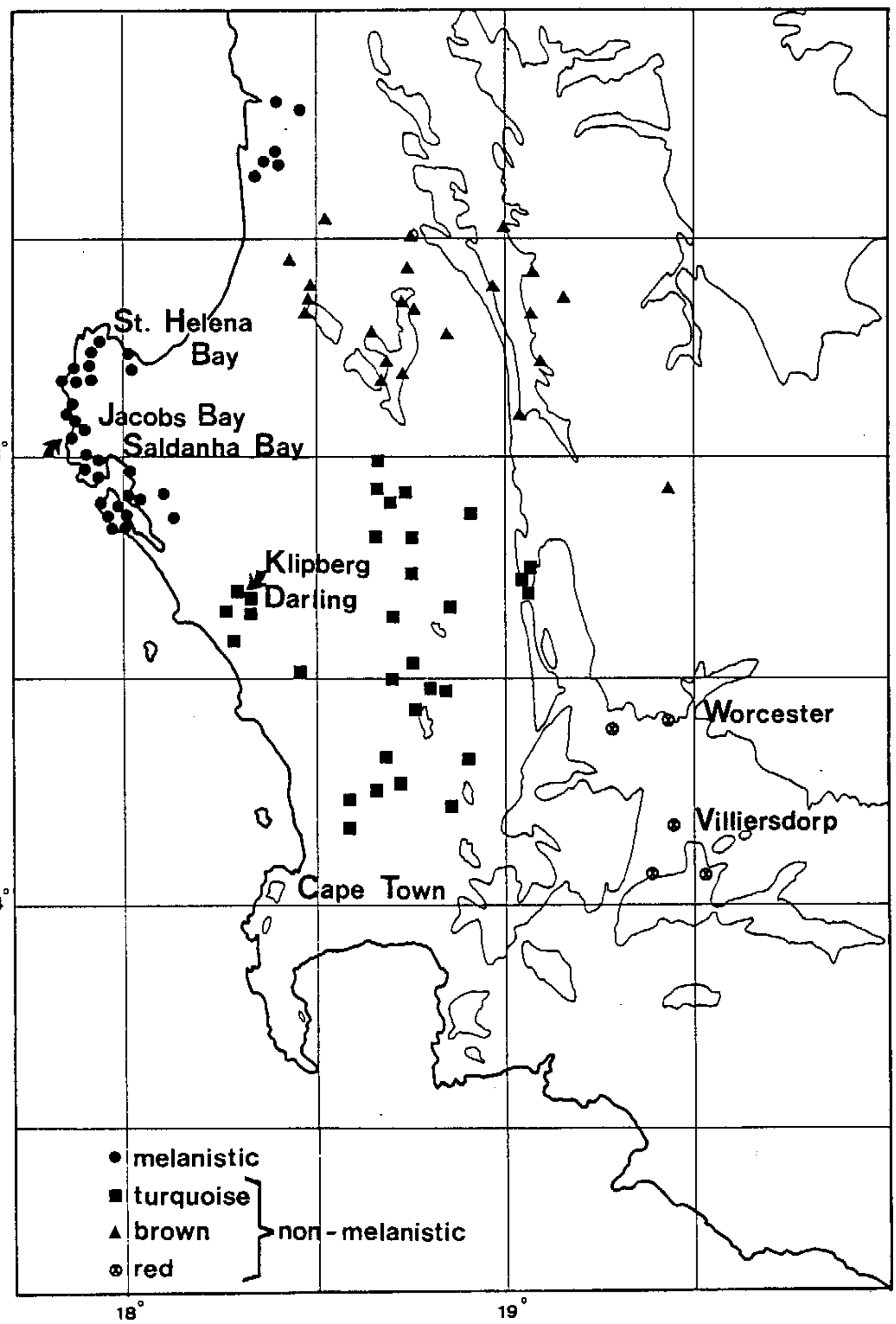
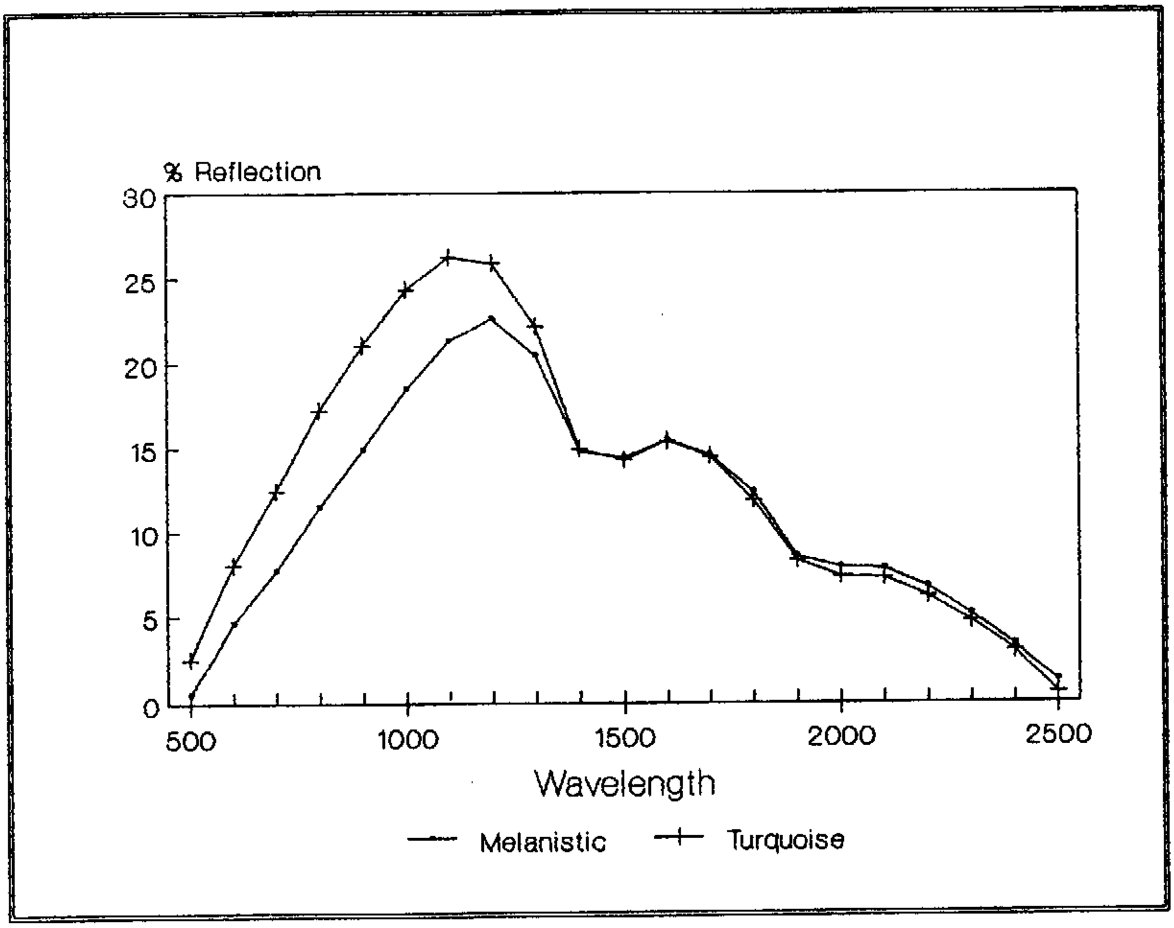

St. Helena
Bay
Jacobs Bay
Saldanha Bay
Klipberg
Darling
Worcester
Villiersdorp
Cape Town
33°
34°
18°
19°
melanistic
turquoise
brown
red
non-melanistic

Figure 1.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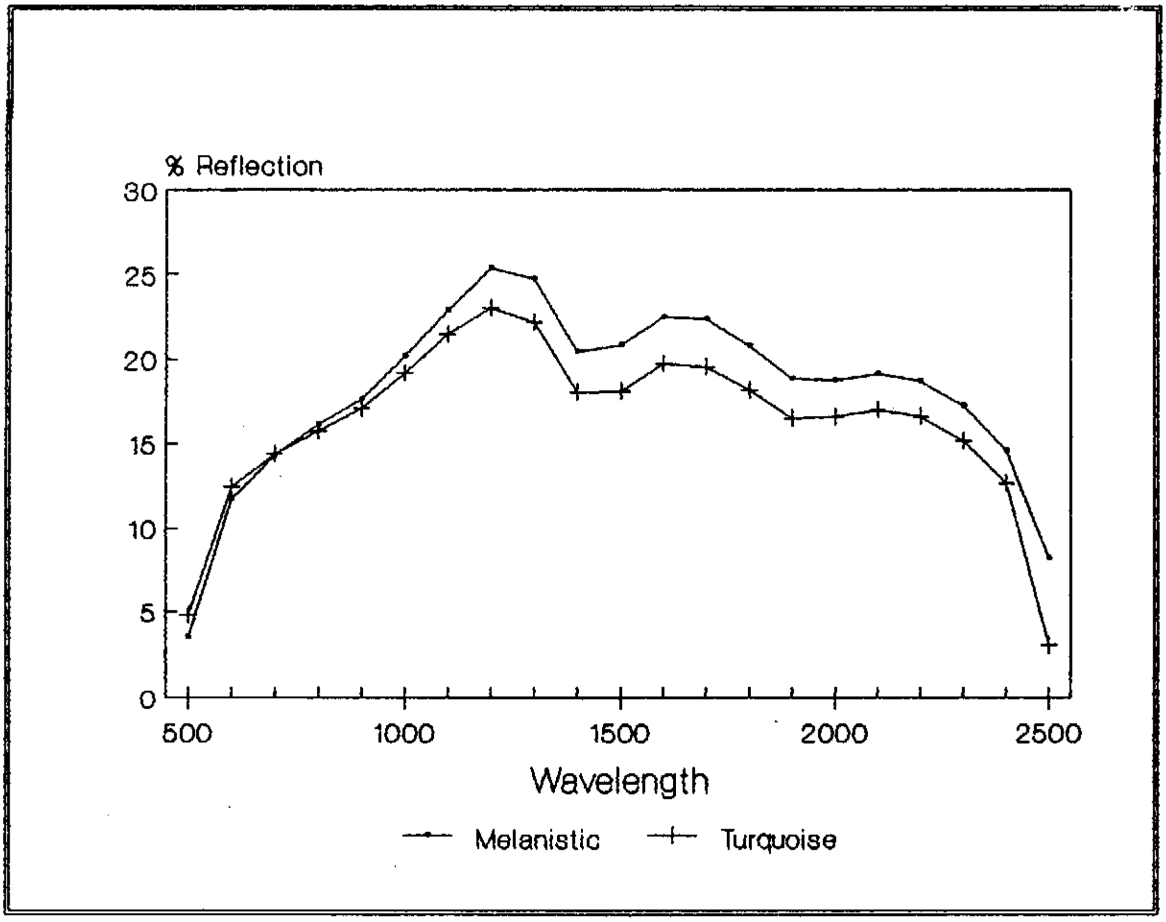
Wavelength
Melanistic
Turquoise

Figure 2.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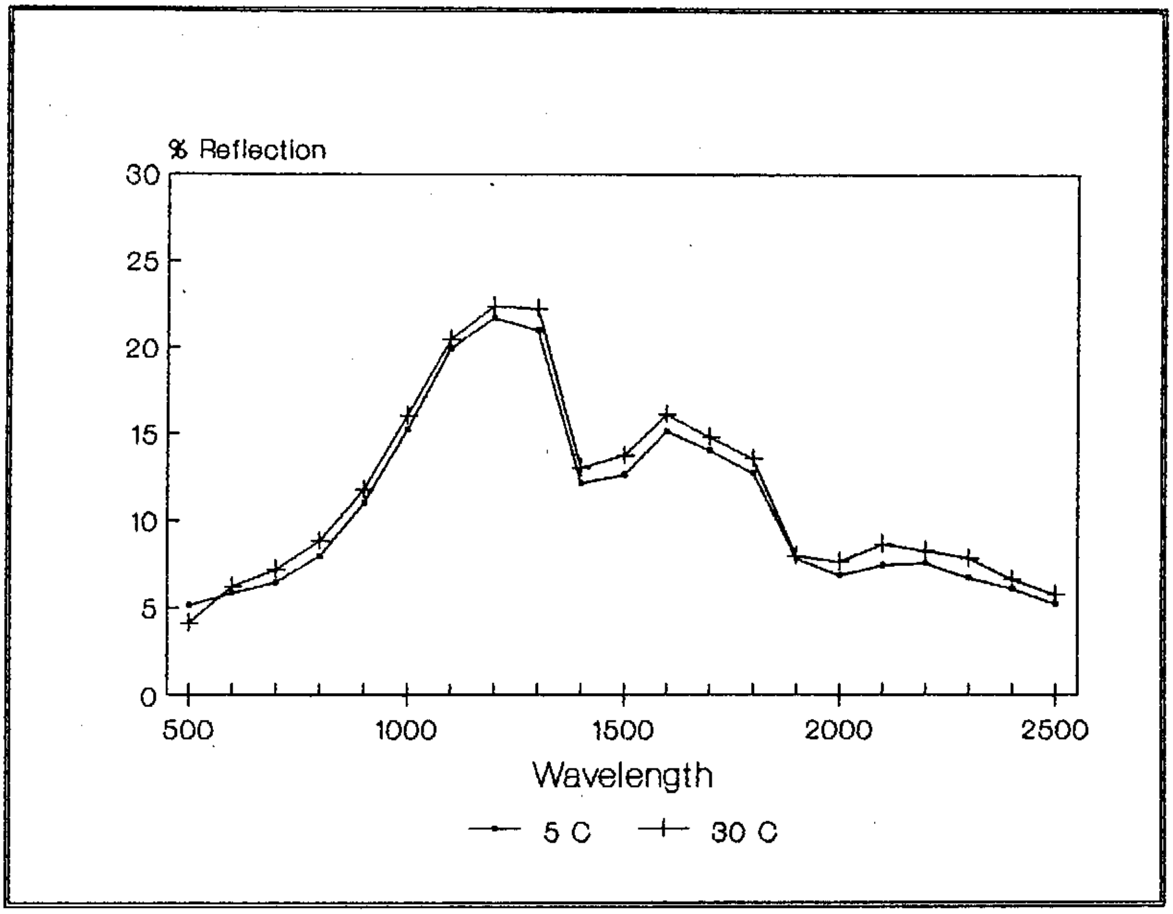
Melanistic
Turquoise

Figure 3.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30 C

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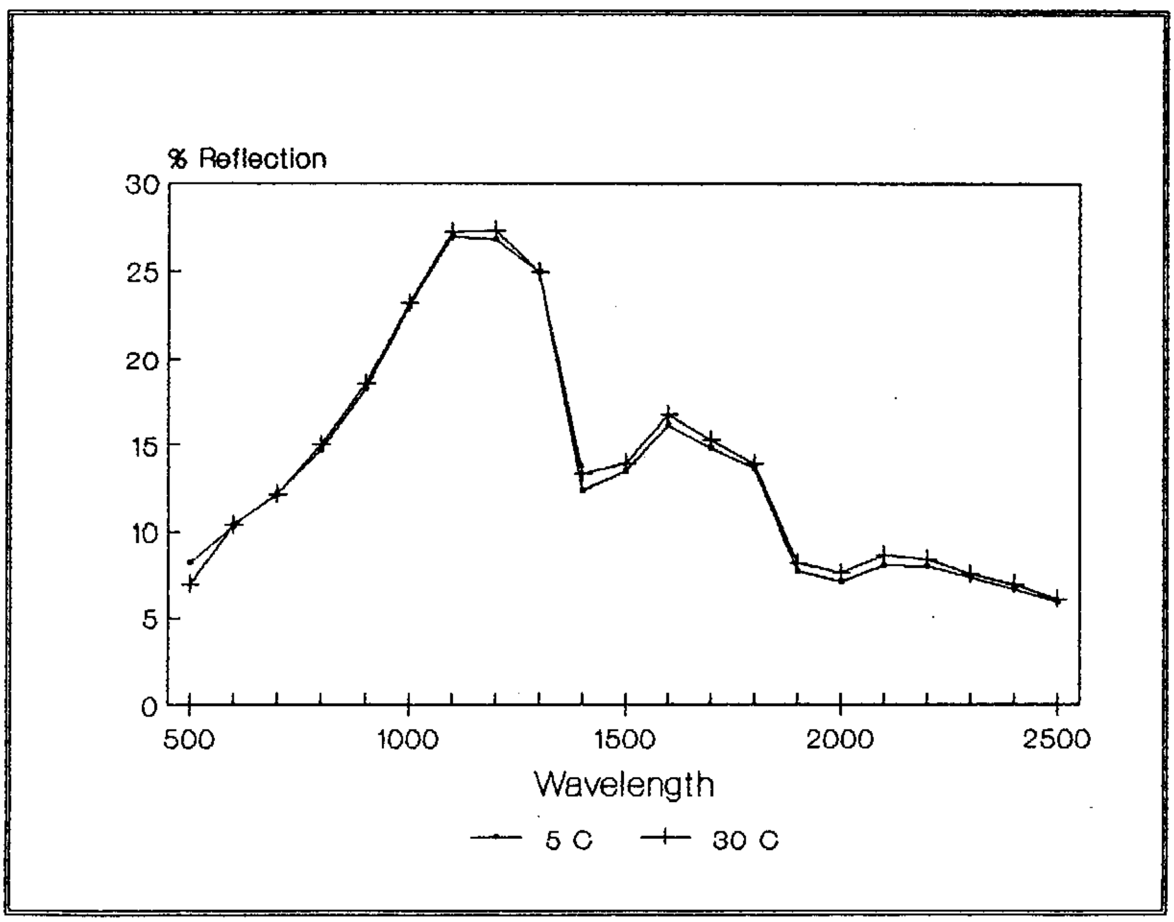
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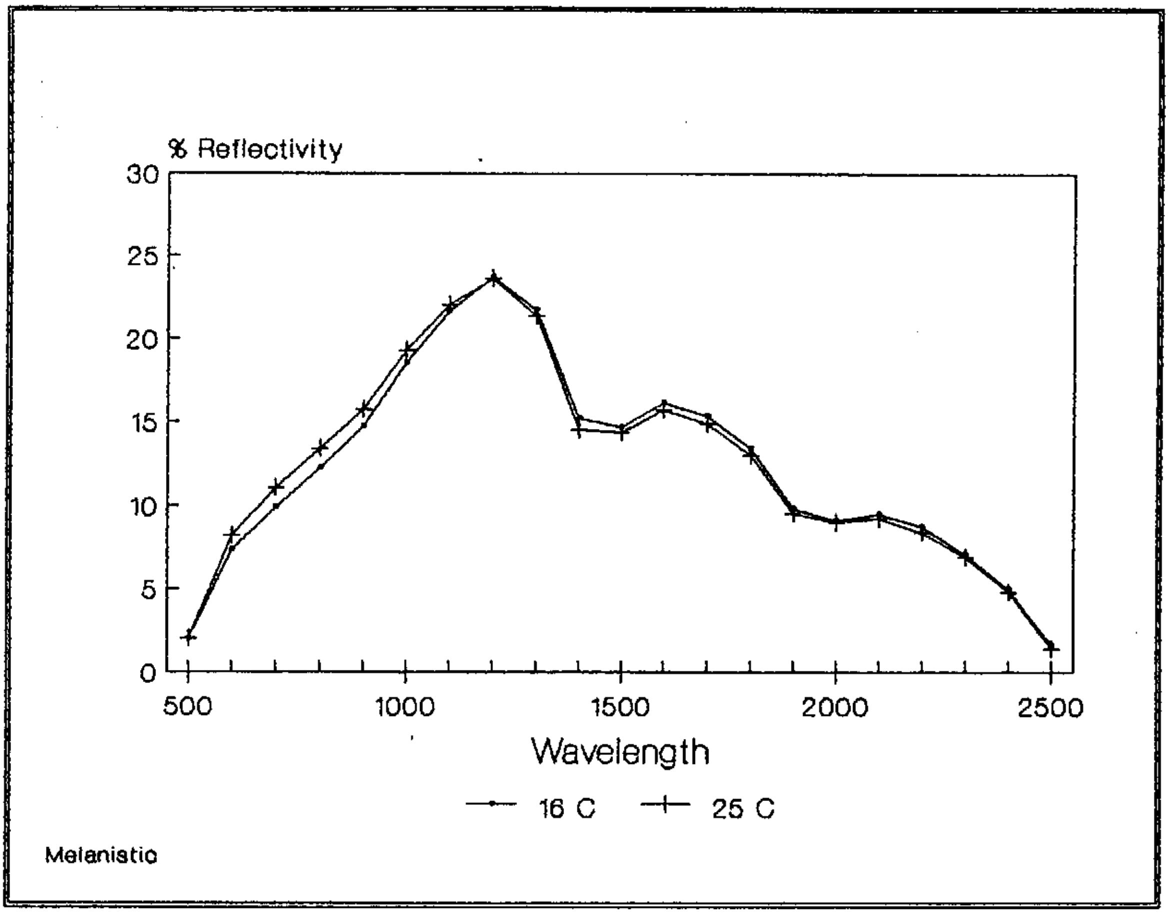
30 C

b

Figure 4.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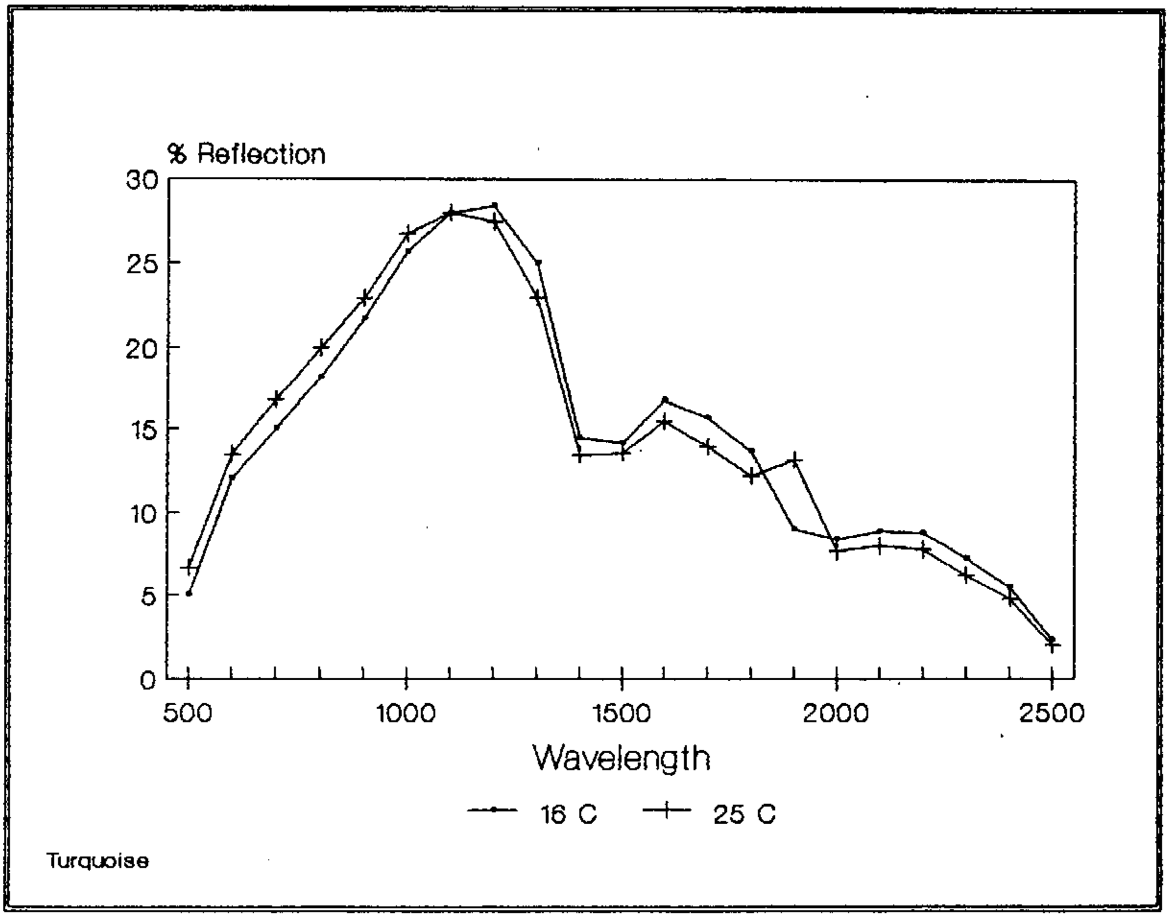
25 C
Melanistic

a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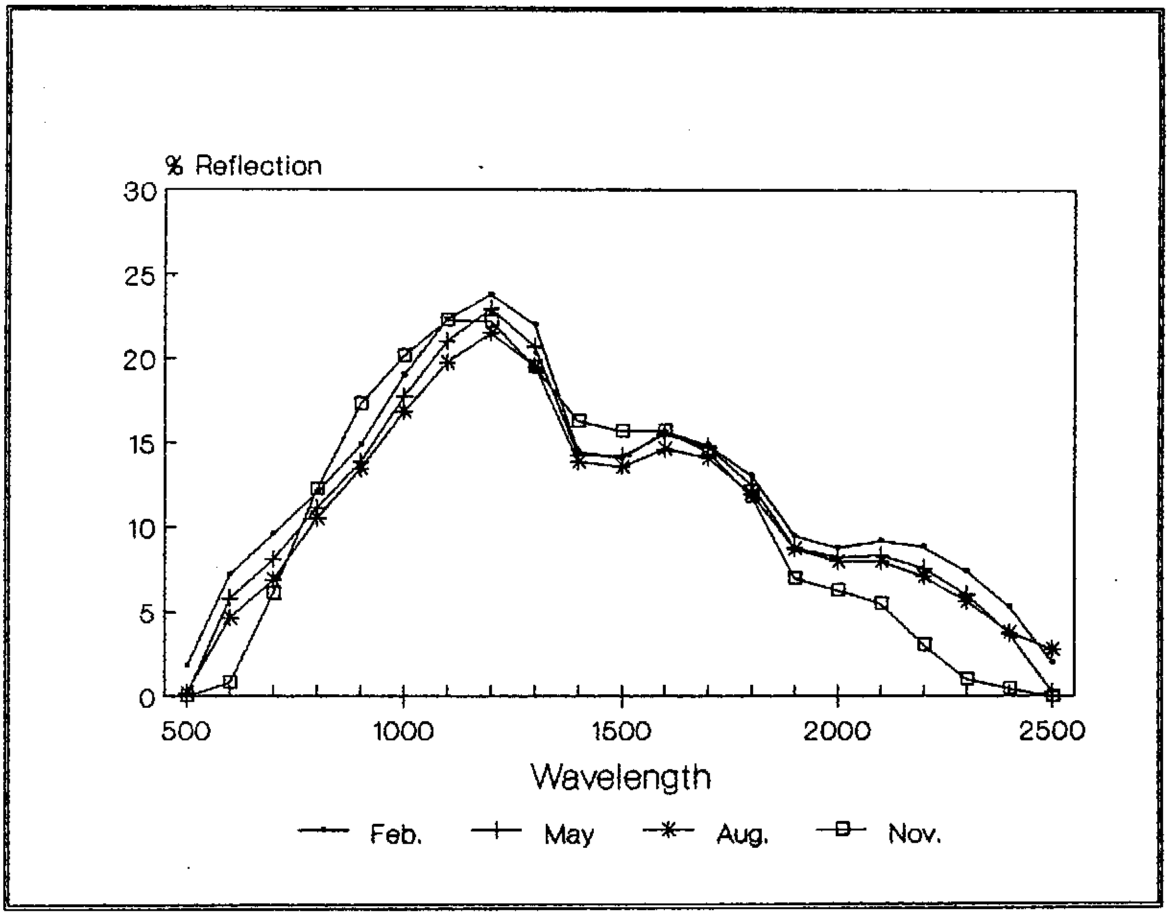
16 C
25 C
Turquoise

b

Figure 5.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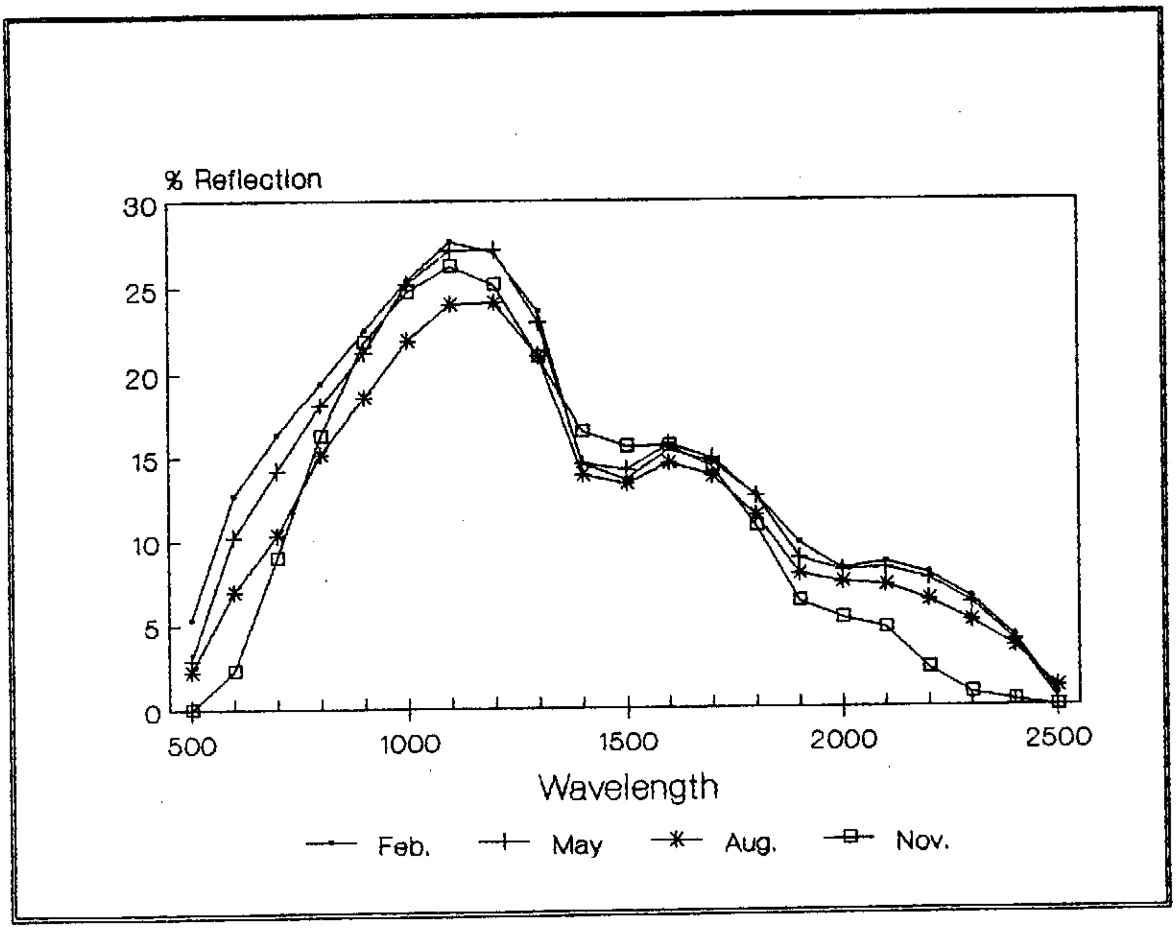
Feb.
May
Aug.
Nov.

a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May
Aug.
Nov.

b

Figure 6.